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### THE GENERA OF EUPHORBIACEAE IN THE SOUTHEASTERN UNITED STATES \*

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Tribe ACALYPHEAE Dumort.

Subtribe Ditaxinae Griseb., "Ditaxideae"

11. *Caperonia* St. Hilaire, Hist. Pl. Remarq. Brésil. 244. 1825.

Annual or perennial herbs, sometimes rhizomatous, often with glandular pubescence. Leaves alternate, undivided, petiolate, serrate, stipulate. Plants monoecious [rarely dioecious]; inflorescences spiciform, axillary, usually bisexual, with 1-5 basal female flowers and several distal male flowers; bracts uniflorous. Male flower: pedicel articulate; calyx usually 5-lobed, lobes valvate in the bud; petals 5, often unequal, basally adnate to the staminal column; disc absent; stamens 10, connate, anthers in 2 superposed whorls; pollen subglobose, reticulate, 6-colporate, germ pores large; vestigial gynoecium terminating the staminal column. Female flower: subsessile [rarely pedicellate]; calyx deeply 5-lobed, with 0-5 smaller supernumerary lobes; disc obsolete; carpels 3; styles 3, more or less deeply 3-7-lobed; ovary usually densely muricate; ovules solitary in each locule, anatropous, nucellus not elongated. Fruit capsular, more or less verrucose; columella slender, apically dilated. Seeds spheroidal, minutely foveolate, with narrow raphe; caruncle absent; endosperm copious; cotyledons broader than radicle. LECTOTYPE SPECIES: *C. castaneifolia* (L.) St. Hil.; see Britton and Wilson, Sci. Surv. Porto Rico 6: 486. 1924. (Named in honor of Noël Capperon, 16th Century pharmacist of Orléans, France, the discoverer of *Fritillaria Meleagris* L.)

A genus of 35 to 40 species, about three-fourths of these native to tropical America and the remainder to Africa. Although placed near *Argythamnia* in most treatments, the plants look very different from that genus because of their serrate leaves with conspicuously parallel lateral veins and simple, often glandular, trichomes (as opposed to the bifurcate trichomes of *Argythamnia*).

A single introduced species, *Caperonia palustris* (L.) St. Hil., is now

\* Continued from volume 48, p. 361.



found in ditches and swampy areas in Texas, Louisiana, and Florida. It belongs to sect. *CAPERONIA* because of its annual habit, prickless stems, and female calyx usually with one or more small supernumerary lobes. Another species, *C. castaneifolia* (L.) St. Hil., was reported from Florida by Small in 1933, apparently on the basis of misdetermined specimens of *C. palustris*. The two species are easily distinguished, as *C. palustris* has conspicuously glandular-pubescent stems, narrow lanceolate stipules, and petals about equalling the calyx in the male flower; whereas *C. castaneifolia* lacks glandular pubescence, has ovate stipules, and the male petals are exerted beyond the calyx. There are no authentic records of *C. castaneifolia* in the continental United States.

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PAX, F. Euphorbiaceae-Acalypheae-Chrozophorinae. Pflanzenreich IV. 147-VI (Heft 57): 1-142. 1912. [*Caperonia*, 27-49.]

#### 12. *Argythamnia* P. Browne, Civ. Nat. Hist. Jamaica 338. 1756.

Herbs or shrubs; stems and foliage with indumentum of bifurcate (malpighiaceous) hairs, tissues often stained with purplish pigment. Leaves alternate, petioles short, stipules small; blades entire or dentate, not glandular. Plants monoecious [rarely dioecious]; inflorescences short, racemiform, bisexual, with one to few basal female flowers; bracts small, uniflorous. Male flowers: calyx [3-]5-lobed, lobes valvate in the bud; petals 5, narrowed to a claw at base, more or less adnate to base of staminal column; disc dissected, segments opposite the calyx lobes; stamens 5-15, monadelphous; anthers 1-2(-3)-seriate; 1-3 filiform staminodia sometimes present atop staminal column; pollen oblate, tectate, tricolpate, bilaterally symmetrical; vestigial gynoecium absent. Female flower: calyx 5-parted, lobes imbricate; petals 5, imbricate, entire, sometimes reduced; disc more or less dissected into sometimes elongated segments; carpels 3; styles free or basally connate, bifid, style-branches more or less dilated at the tips; ovules 1 in each locule, anatropous, nucellus not elongated. Fruit capsular; columella persistent. Seeds subglobose, foveolate to reticulate, caruncle absent; endosperm present; embryo straight, cotyledons broader than the radicle. (Including *Ditaxis* Vahl.) TYPE SPECIES: *A. candicans* Sw. (Name from Greek, *argios*, white, and *thamnos*, shrub; the type species noted by Browne as having white bark.<sup>16</sup>)

<sup>16</sup> The generic name has been variously spelled *Argithamnia*, *Argothamnia*, and *Argyrothamnia*; but Bentham (Gen. Pl. 3: 304) pointed out that the last name was based on Mueller's erroneous derivation from *argyros*, silver. As affirmed by Wheeler (Contr. Gray Herb. 127: 55, 56. 1939), there seems to be no reason why the original spelling should not be followed.



An American genus of about 50 species, mostly tropical but some attaining temperate latitudes in the southern United States and in Argentina. The circumscription adopted here is approximately that of Bentham, who followed Mueller in including *Ditaxis* within *Argythamnia* but excluding *Speranskia*. Pax in 1912 adopted a radical view in which most of Mueller's sections (e.g., *Philyra*, *Chiropetalum*) were treated as genera. The pollen studies of Punt provide some support for Pax's view, since most of the taxa in question have easily distinguishable pollen types. *Argythamnia* is rather closely related to our other genus of Ditaxinae, *Caperonia*. However, it not only differs strikingly in its entire, triplinerved leaves, but is technically separable on the basis of its malpighiaceous hairs, male flowers without a rudimentary gynoecium, three- or four-colporate tectate pollen, and ornamented seeds.

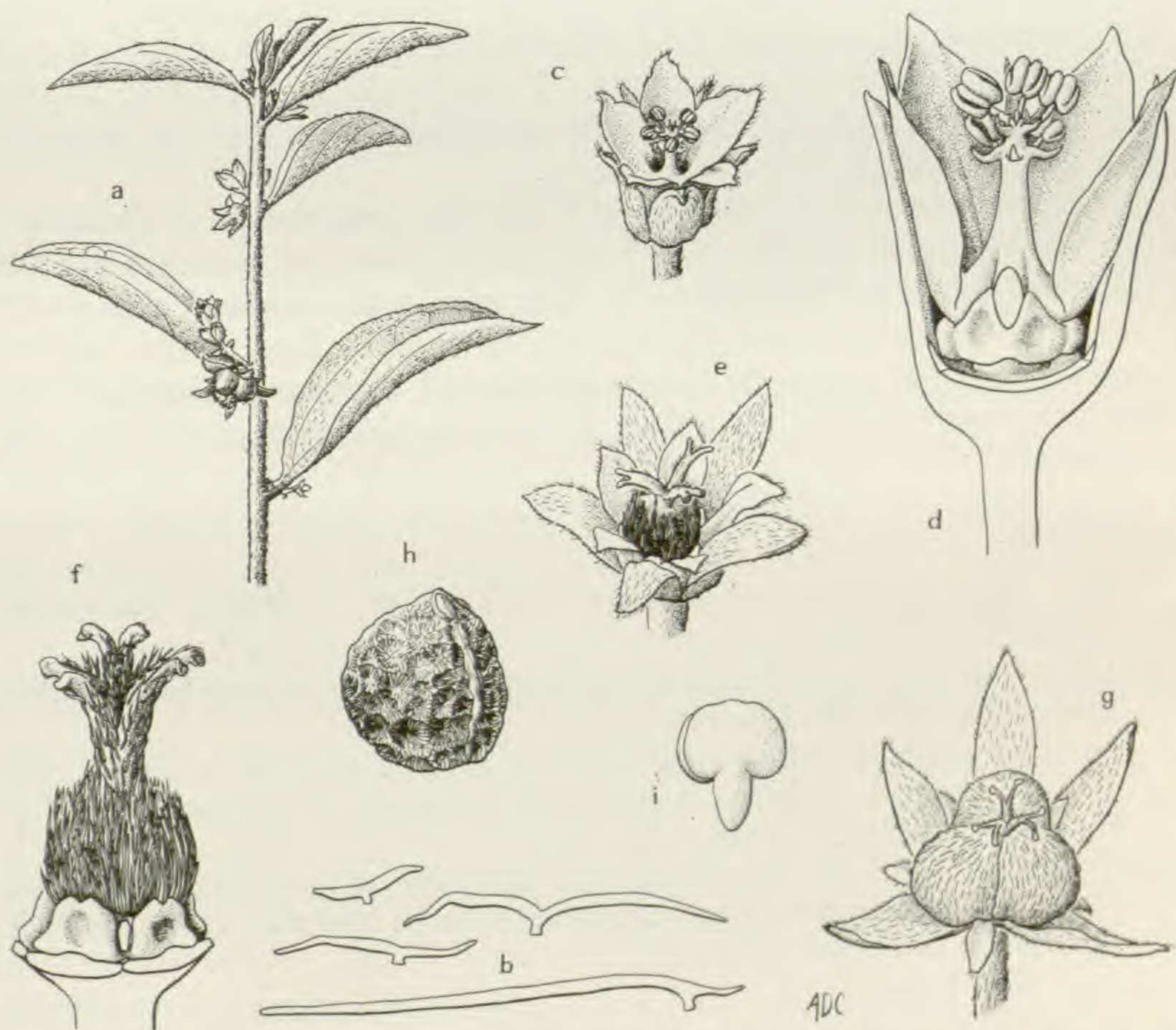


FIG. 3. *Argythamnia*. a-i, *A. Blodgettii*: a, tip of branchlet,  $\times 1$ ; b, malpighiaceous hairs, lateral view, detached from stem and gynoecium,  $\times 100$ ; c, male flower,  $\times 6$ ; d, same, with two sepals, one petal, and five anthers removed to show disc, insertion of petals, and arrangement of stamens in two whorls, the hairs omitted,  $\times 12$ ; e, female flower,  $\times 6$ ; f, same, with sepals and petals removed to show disc and gynoecium,  $\times 12$ ; g, nearly mature schizocarp,  $\times 4$ ; h, seed,  $\times 8$ ; i, embryo,  $\times 8$ .

Our representatives of *Argythamnia* all belong to subg. *DITAXIS* (Vahl) Croizat, which includes the species with a usually biseriate androecium of



approximately 10 stamens and bifid styles (the branches sometimes bilobed). Section SEROPHYTON (Benth.) Webster<sup>17</sup> is represented by two species which have been reported from Arkansas: *A. mercurialina* (Nutt.) Muell. Arg., with elongated inflorescences (over 5 cm. long), petals obsolete or wanting in the female flower, and large (4–5 mm.), wrinkled seeds; and *A. humilis* (Engelm. and Gray) Muell. Arg., with abbreviated inflorescences scarcely 1 cm. long, petals present in the female flower, and small (ca. 2 mm.), reticulate seeds. In Florida, sect. DITAXIS [(Vahl) Muell. Arg.] is represented by *A. Blodgettii* (Torr.) Chapm.; this species differs from members of the preceding section in having the petals adnate to the staminal column. Pax followed Mueller in assigning the Florida plants to *A. Fendleri* Muell. Arg. [= *A. argothamnoides* (Bert.) Ingram], a species otherwise known from South America. The plants involved do look much alike, but differ in various floral details (e. g., petals broader and staminodia ciliate-tipped in *A. Blodgettii*) and in the sculpturing of the seed-coat. Apparently, therefore, *A. Blodgettii* is a distinct species endemic to pine woods and hammocks on limestone in extreme southern peninsular Florida and the Florida Keys.

A single chromosome count of  $n = 13$  has been recorded in *A. Brandegei* Millsp., a species of Mexico. Our local species have not yet been studied cytologically, but if they prove to have the same number, this would provide interesting evidence toward defining relationships in the subtribe Ditaxinae. So far counts in *Chrozophora* and *Caperonia* show  $x = 11$ , indicating a more distinct separation of *Argythamnia* than might otherwise be suspected.

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#### Subtribe Mercurialinae Pax

13. **Mercurialis** Linnaeus, Sp. Pl. 2: 1035. 1753; Gen. Pl. ed. 5. 457. 1754.

Annual [or perennial] herbs [sometimes rhizomatous]; leaves opposite, stipulate, petiolate, more or less pellucid-punctate, with crenate margins. Plants dioecious (rarely a few male flowers developed on female plants)

<sup>17</sup> *Argythamnia* sect. **Serophyton** (Benth.) Webster, comb. nov. *Serophyton* Benth. Bot. Voy. Sulphur 52. 1844.



[or monoecious in some polyploid taxa]; flowers in modified thyrses, the male racemiform or spiciform, the female capituliform-pedunculate; female bracts 1-flowered, male several-flowered. Flowers apetalous. Male flower: calyx closed in bud, splitting into 3 valvate segments at anthesis; disc absent; stamens 8–15 (–20), free, filaments variously oriented in bud, anthers extrorse, anther-sacs subglobose, dehiscing transversely; pollen ellipsoidal, tectate, tricolporate, colpi narrowly operculate; vestigial gynoeceum absent. Female flower: calyx lobes 3, imbricate; disc absent; 2 elongate staminodia usually present; carpels 2 (very rarely 3); styles free except at base, unlobed, conspicuously papillate; ovule 1 in each locule, anatropous, nucellus not elongated. Fruit capsular; valves echinate; columella slender. Seeds not compressed, testa rugose, caruncle present but small and delicate; endosperm present; cotyledons broader than and about equalling the radicle. LECTOTYPE SPECIES: *M. perennis* L.; see Small in Britton and Brown, *Illus. Fl. No. U. S.* ed. 2. 2: 460. 1913. (Classical name used by Pliny to honor the god Mercury, the mythical discoverer of the therapeutic properties of the plant.) — MERCURY.

A small genus of seven or eight Old World species, mostly in the Mediterranean region but with one or two taxa in China, Japan, and Formosa. The genus is similar to *Acalypha* but lacks the highly specialized male flowers of that genus, and it is easily distinguished by its opposite leaves and small female bracts. In fact (cf. Pax, 1914), the closest relationships are probably with three small genera of Pax's series *Mercurialiformes*: *Seidelia* and *Leidesia*, from South Africa, and *Dysopsis*, from the southern Andes. The only species of *Mercurialis* naturalized in the United States is *M. annua* L., which has been reported from widely scattered localities within our area.

It is rather remarkable that a plant as undistinguished in appearance or properties (aside from a few dubious medical virtues) as *M. annua* has had such an outstanding botanical career. It was the first species experimented on by Camerarius (1691) in his demonstration of sexuality in plants; he simply isolated female plants and proved that seeds did not occur in the absence of fertilization. Actually, he may have been lucky in getting positive results, for exactly three centuries later Kerner made the claim that isolated female plants did set seed and that *M. annua* was therefore parthenogenetic. Further investigations showed that Kerner's observations were correct but his explanation wrong. Isolated female plants may indeed produce seeds, but Bitter and Malte showed that megasporogenesis and seed development is normal and that the apparent parthenogenetic fruits are actually produced as the result of fertilization by scattered reduced male flowers on otherwise strictly female plants; these small male flowers develop rapidly and are difficult to detect.

The remarkable variability in sexual expression in mercuries has attracted the interest of many investigators (e.g., Yampolsky), but for a long time no very convincing explanations could be offered. The key to the problem was found only recently, when Durand and Thomas discov-



ered that different kinds of sexual expression were correlated with a remarkable polyploid series within *M. annua* (*sensu lato*). Durand has shown that within the Linnaean *M. annua* there are no less than seven levels of ploidy: from  $2x$  ( $2n = 16$ ) to  $14x$  ( $2n = 112$ ). Strictly dioecious plants are found only in the weedy diploid species, *M. annua* (*sensu stricto*), which is the form immigrant in the United States and elsewhere. In southern France is found a nonweedy diploid plant of dolomitic outcrops, *M. Huetii* Hanby, which may represent the ancestor of the weedy populations. Although treated by Mueller as a variety of *M. annua*, it is reproductively isolated and morphologically distinctive. Along the shores of the Mediterranean in both Europe and Africa occur a large number of polyploid populations which differ in not being perfectly dioecious. Durand has assigned the tetraploid and hexaploid races, which include both monoecious and unisexual plants, to *M. ambigua* L. f., while he has created a new name (invalid in the absence of a Latin description) for the plants at the octoploid level and higher. With these discoveries a considerable insight into population structure in the annual mercuries has been gained, and the stage is now set for a definitive taxonomic revision of the genus.

The work on *Mercurialis* has many interesting implications. Yampolsky, among others, has investigated the remarkable diversity of intersexual flowers in *Mercurialis*: curiously, completely functional hermaphroditic flowers appear to be absent or extremely rare. Thomas speculates that in *Mercurialis*, in which experiments have shown the female to be the heterogametic sex, the Y allosome for maleness functions by inhibiting production of female flowers. The conflicting results of previous investigators may then be at least partially explained by their failure to appreciate the complex interactions between genetic control of sexual expression and the lability of organogenesis as affected by environmental factors. It seems likely that *Mercurialis* may now become a classical organism for more profound studies of the genotype-phenotype relationship.

The reproductive biology of *Mercurialis* demands further study, especially in the field. Although earlier reports of parthenogenesis have been discredited, little is known of pollination in the wild, and reports are conflicting. The flowers have all the earmarks of anemophily (e.g., apetalous, long filaments, papillate styles) and are cited in many textbooks as a standard example of wind pollination. Wettstein described the remarkable mechanism for pollen dispersal, in which the entire male flower dehisces explosively and may be thrown as far as 20 cm. The process of pollen transfer might therefore be described as a combination of wind and "ballistic" pollination. On the other hand, some authors (e.g., Michaelis) have pointed out that the staminodia in the female flower function as nectaries, and the male plant gives off a distinctive odor; visits by flies, thrips, and even moths have been recorded. Weiss thought that *Mercurialis* was originally anemophilous and is in the process of becoming insect pollinated. However, in agreement with Pax & Hoffmann, it would seem that the opposite is more likely true. As in *Castanea*, the flowers of *Mercurialis* seem to have acquired many anemophilous characteristics,



without however entirely losing the potentiality of a certain lesser amount of insect pollination.

Cytological studies have yielded much information of taxonomic and evolutionary interest, as already partly discussed for the *M. annua* complex. The base number in all species investigated of *Mercurialis* is definitely  $x = 8$ , which contrasts with the base numbers of 11 and 13 in subtribe Ditaxinae, and with  $x = 10$  in *Acalypha*, which has been placed close to *Mercurialis* in many taxonomic treatments. So far no other morphologically similar genus with  $x = 8$  has been detected. Gadella & Kliphuis have made a remarkable report that in *M. perennis*  $2n = 64$  in the female and 66 in the male. If confirmed, this would apparently mean that the mechanism of sex inheritance is different from that found in *M. annua*, where there is no difference in number nor any morphologically detectable sex chromosomes.

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Subtribe *Acalyphinae* Griseb., "Acalypheae"

14. *Acalypha* Linnaeus, Sp. Pl. 2: 1003. 1753; Gen. Pl. ed. 5. 436. 1754.

Annual or perennial herbs or shrubs [rarely trees]; indumentum of simple hairs or glands. Leaves alternate, stipulate, petiolate, unlobed, often punctate. Plants monoecious or rarely dioecious; inflorescences spiciform [rarely paniculate], unisexual or bisexual, terminal or axillary; female flowers 1-3 per bract, bracts large and foliaceous, often lobed or parted [rarely small and entire]; male flowers several per bract, bracts very small. Flowers apetalous, disc absent. Male flowers subsessile; calyx valvate, parted into 4 segments; stamens 4-8, filaments free or connate at base; anther-sacs pendent, unilocular, more or less elongated and vermiform; pollen oblate-spheroidal, 3-5-pseudoporate, tectate, psilate; vestigial gynoecium absent. Female flowers sessile; calyx lobes 3[-5], imbricate; carpels 3 (rarely only 1 or 2); styles free or basally connate, laciniate or lacerate into filiform segments [rarely subentire]; ovary smooth, pubescent, or echinate; ovules 1 in each locule, anatropous, sometimes with a short nucellar beak; embryo sac tetrasporic. Fruit capsular, sometimes surrounded by the accrescent female bract. Seeds ovoid, carunculate,



smooth to pitted or tuberculate; endosperm whitish; embryo straight, cotyledons reniform, broader than the radicle. LECTOTYPE SPECIES: *A. virginica* L.; see Small in Britton and Brown, Illus. Fl. No. U. S. ed. 2. 2: 457. 1913. (Name from Greek, *akalos*, unattractive, and *aphe*, touch; Linnaeus's derivation obscure, as the plants he placed in the genus are not stinging.)<sup>18</sup>

A very natural genus of about 400 species, the majority American, and the largest concentration (about 100 species) in Mexico and Central America. The genus is isolated in the Euphorbiaceae, as the only other taxon in the subtribe Acalyphinae is the monotypic *Acalyphopsis*, based on an aberrant species from Celebes. Mueller and others have placed *Acalypha* close to *Mercurialis*, perhaps because of the similarity in habit and wind-pollinated flowers. However, the basic chromosome number and pollen grains are different in the two genera, and the resemblances may prove to be superficial. As suggested by Pax & Hoffmann, the relationship of *Acalypha* probably lies with some group within the subtribe Mercurialinae, but a more exact affinity cannot be pointed out at this time.

The infrageneric classification of *Acalypha* presented by Pax & Hoffmann was modelled closely on that of Mueller, except that the ranks of the subgeneric taxa were inflated so that no less than 40 sections were recognized in place of the two proposed by Mueller. Because of the narrow amplitude of divergence among the species of *Acalypha*, these "sections" of Pax and Hoffmann are really comparable to subsections or series in other genera of Euphorbiaceae, and they are so treated here.<sup>19</sup>

<sup>18</sup> Pax & Hoffmann (Pflanzenreich 147-XVI (Heft 85): 12. 1924) derive the generic name from *akalyphes*, not covering, in apparent allusion to the female bracts; but this is contradicted by Linnaeus's explicit derivation of the name (Philos. Bot. 183).

<sup>19</sup> It is difficult to reconcile the systems of infrageneric taxa erected by students of *Acalypha* with biological reality, on the one hand, and with the requirements of the present Code of Nomenclature on the other. Hurusawa (Jour. Fac. Sci. Univ. Tokyo Bot. 6: 295-301. 1954) has inflated the subgeneric taxa to an even greater (and more unacceptable) extent than did Pax and Hoffmann. Mueller's division of the genus into two sections with many infrasectional taxa appears to reflect degrees of relationship better, but on the basis of his own explanation (Linnaea 34: 2-4. 1865) his ultimate taxa designated by the sign "§" were not subsections but simply "Gruppe." Pax & Hoffmann unwarrantedly treated these groups as though Mueller had published them as sections. Technically, Mueller's names are almost all illegitimate under current rules of nomenclature, but, since his ultimate taxa appear to correspond rather closely to those currently accepted at the rank of "series," they are accepted at this rank here, and presumably are valid from the date of publication of this paper. The ten series occurring in the United States or mentioned in this discussion are then as follows:

(1) Series **Sclerolobae** Muell. Arg., ser. nov.; based on § *Sclerolobae* Muell. Arg. Linnaea 34: 23. 1865. LECTOTYPE: *A. setosa* A. Rich.

(2) Series **Plumosae** Muell. Arg., ser. nov.; based on § *Plumosae* Muell. Arg. loc. cit. 49. LECTOTYPE: *A. alopecuroidea* Jacq.

(3) Series **Phleoideae** Muell. Arg., ser. nov.; based on § *Phleoideae* Muell. Arg. loc. cit. 46. LECTOTYPE: *A. phleoides* Cav.

(4) Series **Brachystachyae** Muell. Arg., ser. nov.; based on § *Brachystachyae* Muell. Arg. loc. cit. 42. LECTOTYPE: *A. brachystachya* Hornem.



Of the 17 species of *Acalypha* recorded from the United States, nine species in four series occur in our area. All of these plants belong to sect. ACALYPHA because of the sessile female flowers with large bracts; the few taxa in sect. LINOSTACHYS (Kl.) Muell. Arg., characterized by pedicellate female flowers subtended by small bracts, occur mostly in tropical America and do not reach our limits.

The basic division of the genus was made by Mueller largely on the basis of the relative position of the female and male flowers, which may be either proximal or distal on terminal or axillary unisexual or bisexual spikes. The group Pantogyne-Acrogynae of Mueller, distinguished by unisexual spikes with the female spike terminal, is represented in our area by ser. SCLEROLOBAE Muell. Arg. ex Webster, which is characterized by narrow female spikes and deeply lobed female bracts. The two local representatives are *A. ostryifolia* Ridd., with 13–17-lobed female bracts, occurring throughout our area; and *A. setosa* A. Rich., with mostly 7–8-lobed female bracts, restricted to the Coastal Plain at scattered localities from South Carolina to Florida and Louisiana. The latter, native to the West Indies and Central America, is strictly a weed in the southeastern United States and appears to have been introduced.

Mueller's group Polygynae-Acrogynae, in which the spikes are usually bisexual and terminal (often with axillary ones as well), is represented by two series, each with a single species. *Acalypha alopecuroides* Jacq., belonging to ser. PLUMOSAE Muell. Arg., and recognizable by its dense, thickly pubescent spikes, has been sparingly introduced into southern Louisiana from tropical America. *Acalypha chamaedrifolia* (Lam.) Muell. Arg., of ser. PHLEOIDEAE Muell. Arg., is a native species restricted in our area to extreme southern Florida and the Keys; its principal distribution is in the West Indies. It is easily distinguished from our other species by the perennial habit and small seeds (usually only about 1 mm. long).

Most of our local plants of *Acalypha* belong to Mueller's group Polygynae-Pleurogynae, in which the spikes are bisexual and strictly axillary. Our four or five species, the weedy members of the notorious *Acalypha virginica* complex, are all annuals referable to ser. BRACHYSTACHYAE Muell. Arg. because of their abbreviated spikes with few female bracts. Weatherby recognized 3 species in this group, one with two varieties;

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(5) Series **Boehmerioideae** Muell. Arg., ser. nov.; based on § *Boehmerioideae* Muell. Arg. DC. Prodr. 15(2): 871. 1866. LECTOTYPE: *A. boehmerioides* Miq. [= *A. lanceolata* Willd.].

(6) Series **Repandae** Muell. Arg., ser. nov.; based on § *Repandae* Muell. Arg. DC. Prodr. 15(2): 868. 1866. LECTOTYPE: *A. indica* L.

(7) Series **Dentatae** Muell. Arg., ser. nov.; based on § *Dentatae* Muell. Arg. Linnaea 34: 17. 1865. LECTOTYPE: *A. mollis* HBK.

(8) Series **Monostachyae** Muell. Arg., ser. nov.; based on § *Monostachyae* Muell. Arg. loc. cit. 53. LECTOTYPE: *A. monostachya* Cav.

(9) Series **Palminerviae** Muell. Arg., ser. nov.; based on § *Palminervia* Muell. Arg. loc. cit. 9. LECTOTYPE: *A. macrostachya* HBK.

(10) Series **Caturoideae** (Pax & Hoffm.) Webster, stat. nov.; based on sect. *Caturoideae* Pax & Hoffm. Pflanzenreich 147-XVI (Heft 85): 139. 1924. LECTOTYPE: *A. Caturus* Blume.



whereas L. Miller more recently has distinguished five species, one with two varieties. The group is taxonomically difficult, and Steyermark has described putative hybrids between three species in Missouri; but hybridization has still not been conclusively demonstrated.

Weatherby in a critical study of typification established that the name *A. virginica* L. is to be associated with the relatively narrow-leaved plant having female bracts cut mostly into 10–14 lanceolate lobes with long, spreading hairs. This species is common in Arkansas, Tennessee, and North Carolina but almost completely avoids the Coastal Plain. Far more abundant, widespread, and weedy is *A. rhomboidea* Raf., which has broader leaves and mostly 7–9-lobed female bracts that lack long hairs. It is common throughout the eastern United States and is the only species which crosses into Canada (in Ontario); in our area it is found both in the highlands and the Coastal Plain but does not enter peninsular Florida. Very similar to *A. rhomboidea* in appearance is *A. Deamii* (Weatherby) Ahles, a sibling species only recently discriminated. It has leaves and bracts much like those of *A. rhomboidea*, but differs in its two- rather than three-seeded fruit and in its larger seeds (2.2–3.2 mm. long *vs.* 1.2–2.0 mm. in *A. rhomboidea*). *Acalypha Deamii* seems to be restricted to more mesophytic sites and is known only from scattered localities in the Mississippi-Ohio River drainage, entering our area in Arkansas and Tennessee.

The most controversial populations in ser. BRACHYSTACHYAE include those to which the name *A. gracilens* Gray has been applied. These are plants with narrow leaves, the margins nearly or quite entire, and with much shallower lobing on the female bracts than is found in *A. rhomboidea* and related taxa.

A still unpublished analysis of this group made by L. Miller indicates that there are at least two major taxa involved. Throughout the Coastal Plain in our area, and in some inland localities as well, occurs ssp. *gracilens*, with leaves crenate-lanceolate and staminate spikes very short. To the west, this population is more or less replaced by an Ozarkian population which extends from central Texas into Oklahoma, Arkansas, and Missouri. Plants of this taxon, which differ in their narrower leaves, long male spikes, and, most strikingly, in having one-seeded instead of three-seeded capsules, may be designated as *A. gracilens* ssp. *monococca* (Engelm. ex Gray) Webster.<sup>20</sup> Lillian Miller regards this taxon as meriting specific rank, and it is possible that further investigation may substantiate her viewpoint. Field studies are needed in eastern Texas and Louisiana, where there are plants with the narrow leaves and long male spikes of ssp. *monococca* combined with the 3-seeded capsules of ssp. *gracilens*. These plants have been interpreted by Miller as an undescribed variety of *A. gracilens*, but the alternative explanation (followed here) is that this more or less intermediate population may represent a transition between the two subspecies. Additional studies of the natural populations may eventually provide a generally acceptable answer.

✓ <sup>20</sup> *Acalypha gracilens* ssp. *monococca* (Engelm. ex Gray) Webster, stat. nov. *A. gracilens* var. *monococca* Engelm. ex Gray, Man. Bot. No. U.S. ed. 2. 408. 1856.



Cytological studies in *Acalypha* have so far led to conflicting results, since earlier workers such as Perry and Landes reported  $x = 7$ , whereas more recent reports (Kapil; Miller; Miller & Webster) suggest a base number of  $x = 10$ . Miller found  $2n = 40$  in *A. virginica*, *A. Deamii*, and *A. monococca*, which suggests that at least the taxa of ser. BRACHYSTACHYAE are tetraploids. Miller & Webster found both tetraploid and octoploid levels among three tropical American species.

Perhaps the most interesting aspect of reproductive biology in *Acalypha* is its embryology. In contrast to most genera of Euphorbiaceae, only tetrasporic embryo sacs have been reported in *Acalypha*, and these are of several different kinds; reviews of embryo-sac diversity have been provided by Mukherjee and by Kapil, among others. According to Mukherjee the basic type of female gametophyte in *Acalypha* is the *Penaea* type, in which the mature embryo sac typically contains four egg-apparatuses (each of three cells) and four polar nuclei; this type has been reported in *A. rhomboidea* by Landes, as well as in several Asiatic species. In *A. indica* L. there are eight polar nuclei which fuse, and the four lateral groups are two-celled (Maheshwari & Johri). Finally, there is a report in *A. lanceolata* Willd. of the *Peperomia hispidula* type, in which there is one two-celled egg-apparatus and a  $14n$  polar fusion-nucleus.

The taxonomic implications of this diversity are obscure, partly because of problems in identification. For example, Banerji reported the *Acalypha indica* type in *A. fallax* Muell. Arg.; that name, however, is a synonym of *A. lanceolata* Willd., of ser. BOEHMERIOIDEAE, in which Thatachar reported the *Peperomia hispidula* type. Furthermore, the results so far do not correlate well with the system of Pax & Hoffmann. In *A. malabarica* the embryo-sac is of the least specialized *Penaea* type, whereas in the closely related *A. lanceolata* the presumably most specialized *Peperomia hispidula* type has been reported. In a similar, although somewhat less disconcerting manner, *A. australis* L. and *A. indica* L. are reported to have the *Penaea* type and *A. indica* type respectively, even though they are closely related species of ser. REPANDAE. It may therefore be questioned whether the embryological results thus far throw any light on evolutionary relationships within the genus. However, further studies on a wider range of carefully identified taxa, especially on the less specialized representatives of sect. LINOSTACHYS, are needed before we can dismiss the embryological work as completely irrelevant taxonomically.

In marked contrast with most other sizeable genera of Euphorbiaceae, *Acalypha* is almost devoid of species with economic utility, although various species are cultivated as tropical ornamentals. *Acalypha Wilkesiana* Muell. Arg., a rather unattractive species of ser. PALMINERVIAE Muell. Arg., probably of Fijian origin, is grown presumably because of its variegated foliage. Much more striking is *A. hispida* Burm f., of ser. CATUROIDEAE (Pax & Hoffm.) Webster, possibly of Papuan origin, which has attractive reddish female spikes. Both are grown in southern Florida, but there is no evidence that either has become naturalized.



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## Subtribe Plukenetinae Pax

15. *Tragia* Linnaeus, Sp. Pl. 2: 980. 1753; Gen. Pl. ed. 5. 421. 1754.

Perennial herbs, sometimes suffrutescent, decumbent to erect or twining; indumentum of uniseriate hairs, stalked glands, and stinging hairs. Leaves alternate, stipulate, petiolate or sessile, entire to more commonly toothed or lobed [rarely divided]. Plants monoecious; inflorescences racemiform, bisexual, opposite the leaves or terminal on lateral branches; female flowers at 1 to several proximal nodes, remaining nodes male; bracts small, subtending solitary flowers. Flowers apetalous, calyx 3–6-lobed, disc absent. Male flower: pedicel articulate; calyx lobes valvate; stamens 2–5 (–8) [–50]; filaments connate at least at base, anthers dehiscing longitudinally; pollen spheroidal, finely reticulate, tricolpate with colpi operculate, or inaperturate; rudimentary gynoecium small or absent. Female flower pedicellate; staminodia absent; carpels usually 3; styles 3, united at least at base, unlobed, often papillate; ovary hispid with stinging hairs; ovules 1 in each locule, anatropous, nucellus not beaked. Fruit capsular; columella persistent, with 3 apical interocular points. Seeds subglobose, smooth or slightly roughened, not carunculate; endosperm whitish; cotyledons foliaceous, considerably broader than the terete radicle. LECTOTYPE SPECIES: *T. volubilis* L.; see Small in Britton and Brown, Illus. Fl. No. U.S. ed. 2, 2: 458. 1913. (Name in honor of the German herbalist Hieronymus Bock, 1498–1554, whose name was latinized as *Tragius*.)

A rather protean genus of more than 100 species found mostly in the tropical regions of Africa and Latin America, but with a few in warm-temperate areas. The intrageneric diversity of *Tragia* is indicated by Mueller's recognition of 12 sections, nine of which were retained by Pax & Hoffmann. Various segregates, such as *Ctenomeria*, have been recognized in the past, and the generic limits still present an interesting problem for study. Punt pointed out that the taxa in sect. *BIA* (Kl.) Muell. Arg. have nonaperturate pollen and suggested that this group possibly might warrant generic status. The discovery of a somewhat transitional kind of pollen in some species of the United States (Miller; Miller & Webster) favors the retention of *Bia* within *Tragia*, but the issue can still not be regarded as settled.

To some extent, the taxa of *Tragia* in the United States represent the outliers of mainly tropical groups, but there are several species which are primarily of eastern temperate North American origin. Both sections found in the United States are represented in the southeastern United States. Section *TRAGIA*, which includes those species with mainly 3–5 stamens and tricolpate pollen grains, is represented by 11 species in the United States. These include the weedy “nose-burns” characteristic of disturbed areas in Texas and adjacent states, which Johnston interpreted as all belonging to a single species, *T. nepetifolia* Cav. In the judgment of Miller & Webster, however, that species is restricted to Mexico and Arizona, while some of the taxa reduced to synonymy by Johnston are accepted as



distinct species. Five species of sect. *TRAGIA* enter our area; the commonest is *T. urticifolia* Michx., found from North Carolina to Texas and Arkansas and barely entering northern Florida. It occurs mostly in the Piedmont and foothill regions and enters the Coastal Plain at only a few points. It is easily separated from related species by the long, persistent base of the staminate pedicel, which equals the bract (in other species it is much shorter); and it often has conspicuously hispidulous stems.

Two species which superficially resemble *T. urticifolia* enter our area from the west in Arkansas. *Tragia ramosa* Torr., which includes the majority of populations placed in *T. nepetifolia* by Johnston, is an extremely variable species which may, however, be generally recognized by its small female calyx lobes (shorter than the gynoecium) and its typically narrow (sometimes even linear) upper leaves. Often confused with it is *T. betoniciifolia* Nutt., which has broader leaves like those of *T. urticifolia* and a larger female calyx with lobes which extend above the tips of the styles. More isolated both geographically and morphologically is *T. saxicola* Small, which has very slender, wiry stems and broad, sharply toothed leaves; the female flowers and seeds are smaller than those of *T. betoniciifolia*, which it somewhat resembles. It is restricted to pine woods growing on limestone in the Florida Keys and the adjacent Florida mainland.

Occupying a rather divergent position among our species of *Tragia* is *T. cordata* Michx., a twining vine with large deeply cordate leaves and large seeds (more than 4 mm. long). Although widespread, it has a spotty distribution and seems nowhere very abundant; in our area it is known from a few localities in Arkansas and Louisiana, east to Tennessee, Georgia, and extreme northwestern Florida. It appears to be distinctly less weedy than other species and is probably restricted to relatively undisturbed tracts of deciduous forest.

Our two other species of *Tragia* constitute the section *LEPTOBOTRYS* (Baill.) Pax, which is nearly confined to our area. *Tragia urens* L., extending from southeastern Virginia to southern Florida and west to eastern Texas, is the most abundant representative of the genus on the Coastal Plain. Uniquely, it has terminal inflorescences (on lateral leafy twigs) and very characteristic leaves which are entire to irregularly lobed but never sharply toothed as in many congeners. The entire-leaved forms have been recognized as a distinct species *T. linearifolia* Ell., but such a separation seems unjustified. *Tragia Smallii* Shinnars, although having the androeceum and pollen of *T. urens*, differs strikingly in its broader, distinctly toothed leaves and in its inflorescences, which are opposite the leaves, as in all other temperate North American taxa of *Tragia*. It is primarily a species of the Gulf Coastal Plain, being found in open sandy places from central Florida west to extreme eastern Texas. In contrast with members of section *TRAGIA* both of these species have two stamens and pseudocolpate pollen.

Miller (1963) reported the first chromosome counts in the genus, and chromosome numbers are now known for six species. In both sect. *TRAGIA* and sect. *LEPTOBOTRYS* the basic number is apparently 11, as five species



are tetraploids with  $2n = 44$ ; an extralimital species, *Tragia amblyodonta* (Muell. Arg.) Pax & Hoffm., is apparently a decaploid, with  $2n = \text{ca. } 110$ . Unfortunately, the significance of these counts cannot be evaluated at the generic level, since not a single other genus of this subtribe has been studied cytologically.

Pollinating mechanisms are still scarcely known in *Tragia*, but one curious feature of the reproductive biology has now been detected in several species. Ule long ago pointed out that some South American twining plants of *Tragia* (*T. volubilis* L. vel aff.) produce dimorphic fruits: in addition to the usual three-locular capsules there are some indehiscent one-seeded fruits which have two or three long horns. Miller found similar fruit dimorphism in the North American *T. brevispica* Engelm. & Gray; here the production of two kinds of fruit is an important taxonomic character, since it provides one of the main distinctions between that species and the very similar *T. ramosa*, which never seems to produce aberrant capsules. In *T. brevispica* the one-seeded, winged fruits develop from a three-locular ovary with normal ovules, but two of these abort and the outer part of the ovary wall develops unequally to produce the wings. Although Ule rather naively suggested that the winged fruits functioned to raise the plants' competitive ability through animal dispersal, the role the fruits actually play during the life cycle has not yet been elucidated. In a number of South American species horned or crested three-locular fruits occur, as illustrated for *T. Paxii* Lourt. & O'Don., so that a tendency to produce "aberrant" fruits appears to be widespread in the tropical American taxa of the genus.<sup>21</sup> The distinctive stinging hairs of *Tragia* were studied by Knoll and found to be of subepidermal origin. Their structure is unique and unlike the nettle-hairs of *Cnidoscolus* and various Urticaceae, because in *Tragia* the stinging element is a large, sharp-pointed crystal which represents one arm of a highly modified druse. Such a crystal type is found in no other family, and the other genera of Euphorbiaceae possessing it (e.g., *Cnesmosa*, *Acidoton*, and *Dalechampia*) are probably all related to *Tragia*.

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<sup>21</sup> Hauman, on the basis of observations in Argentina, claimed that the winged fruits observed by Ule were teratological (i.e., galls resulting from infestation by a cecidomyid larva). As far as the North American plants are concerned, however, this explanation is highly improbable, since microtome sections of a considerable number of fruits failed to disclose any evidence of insect attack, and winged fruits regularly developed on plants of *Tragia brevispica* grown in the greenhouse.



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Subtribe **Ricininae** Griseb., "Ricineae"

16. **Ricinus** Linnaeus, Sp. Pl. 2: 1007. 1753; Gen. Pl. ed. 5. 437. 1754.

Shrub or tree (annual in temperate regions); twigs smooth, usually glaucous; sap watery. Leaves alternate; stipules fused into a caducous sheath, leaving a circumaxial scar; petiole elongated, with patelliform glands at least at base and at junction with blade; lamina peltate, palmately 7-11-lobed, lobes serrate. Plants monoecious; inflorescences paniculate, terminal (appearing opposite the leaves and axillary due to sympodial growth), proximal nodes with several-flowered male cymules, distal bisexual or female (the bisexual with female flowers central and males lateral); bracts papery, glandular at base. Flowers apetalous, disc absent. Male flower: calyx completely synsepalous in bud, valvately 3-5-partite at anthesis; anthers extremely numerous, up to 1000; filaments partially connate at base, irregularly branched; anthers introrse in the bud; pollen spheroidal, tectate (psilate), tricolporate, colpi narrow; rudimentary gynoecium absent. Female flower: calyx similar to the male, usually caducous; carpels 3; styles connate below, bifid, style-branches usually conspicuously papillate; ovary spinose-muricate; ovules 1 in each locule, anatropous, chalazal region vascularized, nucellus narrowed but not distinctly beaked. Fruit capsular, echinate (rarely smooth); columella wing-dilated above. Seeds somewhat compressed, smooth, usually mottled, carunculate; endosperm copious; embryo straight; cotyledons foliaceous, basally cordate, palmately veined, much longer and broader than the radicle. TYPE SPECIES: *R. communis* L. (Name said to come from the Latin word for tick, suggested by the appearance of the seed.) — CASTOR BEAN.

A genus of a single highly variable species native to Africa and perhaps to India. Mueller distinguished 15 "varieties" and a number of forms which are really cultivars; it is not clear (and probably never will be) whether the species ever showed geographic subspeciation. Because of the economic importance of the seeds, *Ricinus* has received considerable at-



tention from botanists, and it has become a classical experimental plant during recent years. The seeds are valuable for their high content (50 per cent or more) of castor oil, which is a mixture of ricinoleic acid and smaller amounts of oleic, linoleic, and other fatty acids. The unique properties of ricinoleic acid, which thus far has not been isolated from any other plant, have led to the use of castor oil, not only as the familiar purgative, but in many industrial applications (e.g., in the manufacture of paints, inks, plastics, soaps, and linoleum). Almost all of the castor oil used in the United States today is imported, although the plant was grown as a crop

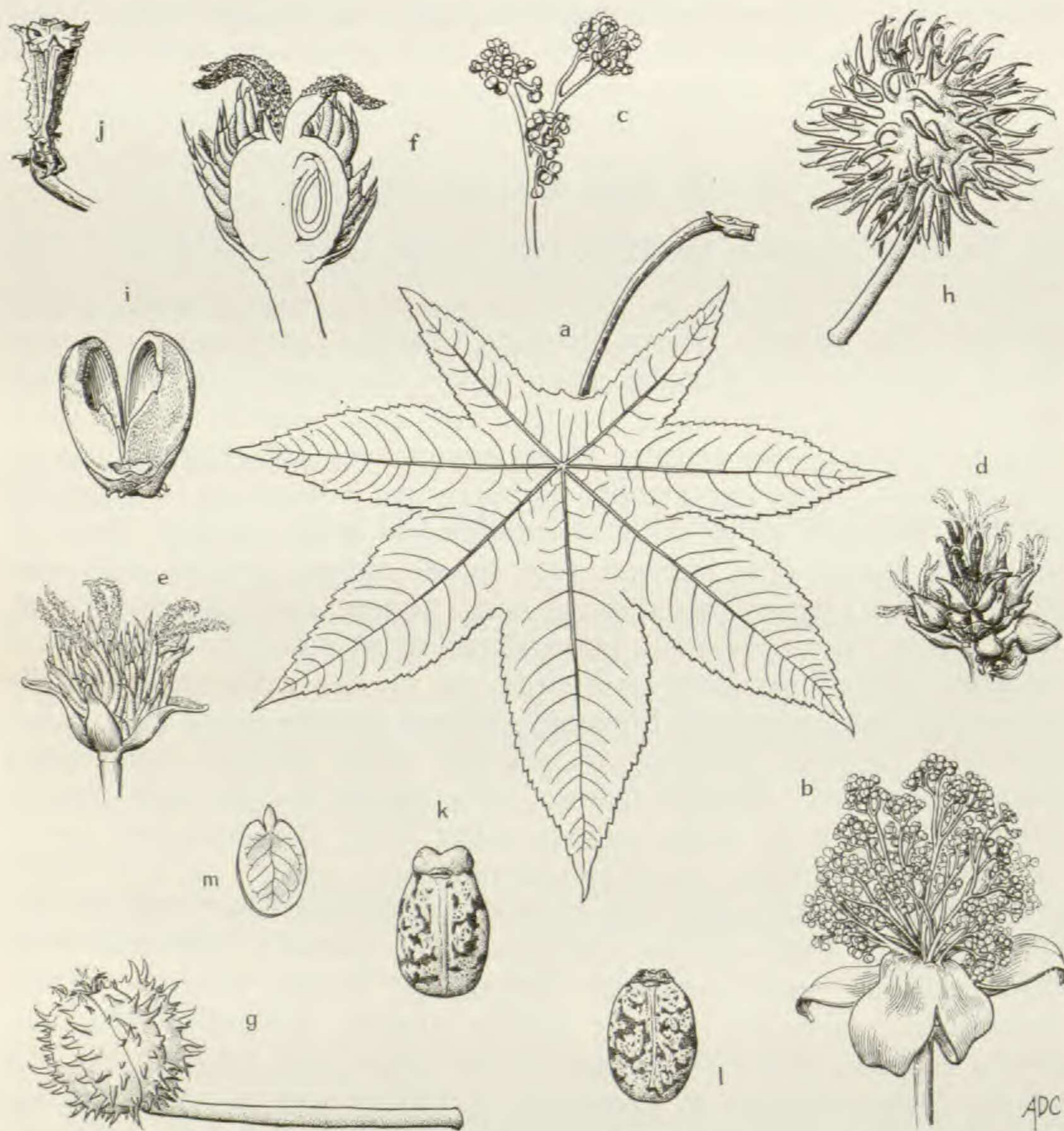


FIG. 4. *Ricinus*. a-m, *R. communis*: a, small leaf,  $\times \frac{1}{2}$ ; b, male flower,  $\times 2$ ; c, detail of stamen fascicle,  $\times 4$ ; d, tip of inflorescence showing female flowers,  $\times 1$ ; e, female flower,  $\times 2$ ; f, same in semidiagrammatic vertical section — note two-integumented anatropous ovule with obturator reaching to micropyle,  $\times 4$ ; g, h, nearly mature fruits from two populations to show variation in fruit surface and pedicel length,  $\times 1$ ; i, carpel wall after dehiscence of schizocarp,  $\times 1\frac{1}{2}$ ; j, columella,  $\times 1\frac{1}{2}$ ; k, l, seed before and after drying of caruncle,  $\times 1\frac{1}{2}$ ; m, embryo oriented as in seed,  $\times 1\frac{1}{2}$ .



in the Midwest during the 19th century, and the industry has revived to some extent at the present time. In our area, climatic conditions permit successful cultivation of *Ricinus* only in Arkansas and western Tennessee, as a serious fungal disease prevents it from being cultivated on the Gulf Coastal Plain. The plant is commonly grown as an ornamental, however, and escaped individuals may be expected throughout most of our range. In the tropical area of southern Florida the plant attains its normal wild expression and becomes a sizable tree very different in appearance from the usual garden herb.

It is well known that the seeds (specifically, the seed-coats) of *Ricinus* are extremely poisonous. This is due not to the alkaloid, *ricinine*, but rather to the phytotoxin, *ricin*, which is one of the most toxic compounds known: the minimum lethal dose by injection is only 0.001 mg. per kg. It is interesting that similar phytotoxins have been reported in the seeds of *Jatropha Curcas* and *Aleurites Fordii*, but our present inexact knowledge of the structure of these complex proteins does not permit placing much taxonomic significance on the distribution of the substances.

Various aspects of the morphology of *Ricinus* have been investigated, especially the remarkable androecium. Delpino called attention to the explosive dehiscence of the anthers, which is similar to that in some Urticaceae, and Steinbrinck and others have seen a resemblance between the *Ricinus* microsporophyll and that of pteridophytes; suggestions have even appeared that the *Ricinus* androecium is a mass of dichotomizing telomes! Such woolly speculations have been effectively discredited by Van der Pijl, but the fascicle-formation of the stamens still has not received a satisfactory explanation.

Various assertions of myrmecophily have been made for *Ricinus*, but the plant has not been sufficiently studied in the wild state, and the significance of the various observations is not clear. The extrafloral nectaries found on the leaves and bracts secrete noticeable quantities of nectar, and Reed has reported visits by ants. Gates has speculated that the caruncle on the seed is attractive to ants, but no observations of large tropical ants carrying off the seeds have been published. The flowers seem to be the most completely anemophilous of any Euphorbiaceae in our area, and, since the seeds are explosively dispersed, any role of animals in the reproductive cycle would appear to be quite hypothetical.

Considerable work has been done on the genetics of *Ricinus*, partly in the attempt to improve its characteristics as an economic plant. The tendency of the capsules to shatter, as in most other Euphorbiaceae, makes mechanical harvesting very difficult and has motivated geneticists to breed for slow-dehiscing fruits. Sex inheritance has also been worked on, although not to the same extent as in *Mercurialis*. Plants which are female in early ontogeny have been obtained, but these eventually produce male flowers, and truly dioecious strains of *Ricinus* are extremely rare, if they exist at all.

Jakob has found evidence of secondary association between two of the ten pairs of chromosomes. This might suggest that the chromosome com-



plement was originally  $x = 9$ , but the cytological evidence is equivocal, and secondary association was not observed among the 10 chromosomes in haploid plants (Poole & Hadley).

*Ricinus* seems to be related to the Asiatic genus *Homonoia*, which was associated with it in the subtribe Ricininae by Pax & Hoffmann; *H. javensis* (Blume) Muell. Arg., in particular, has similar male and female flowers, but its habit is utterly different. The evidently wind-pollinated flowers and chromosome complement of  $x = 10$  suggest a possible distant relationship to *Acalypha*. The lobed, glanduliferous leaves and large, foliaceous cotyledons might appear to suggest an affinity with *Jatropha*, but that seems negated by the differences in androecium, pollen, chromosome number, and many other characters.

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Tribe HIPPOMANEAE Bartl. ex Endl.

Subtribe **Hippomaninae** Muell. Arg.

17. **Sebastiania** Sprengel, *Neue Entdeck. Pflanzenk.* 2: 118. *pl.* 3. 1821.

Shrubs [or trees, rarely herbs]; twigs glabrous or with simple hairs [spinescent in some species]. Leaves alternate [very rarely opposite], stipulate; petiole short; blade undivided. Plants monoecious [rarely dioecious]; flowers in usually bisexual spikes which are terminal or (due to sympodial growth) opposite the leaves [rarely axillary]; female flowers solitary in axils of lower bracts, male flowers usually in clusters of 2 or 3 subtended by upper bracts; bracts biglandular at base. Flowers apetalous, disc absent. Male flower: calyx synsepalous, lobes usually 3 (2), subequal [sometimes distinctly unequal], imbricate; stamens [2 or] 3; filaments free or nearly so, anthers extrorse; pollen subglobose, tectate (psilate), tricolporate, 3-lobed in polar view; rudimentary gynoecium absent. Female flower subsessile; calyx 3-lobed, lobes imbricate, with minute adaxial processes at base; carpels 3 [rarely 2]; styles free or connate at base, entire; ovary smooth [sometimes muricate]; ovules 1 in each locule, anatropous. Fruit capsular; columella dilated above, usually persistent. Seeds subglobose [cylindric in some species], smooth [or roughened], carunculate; endosperm copious; embryo straight, cotyledons broader and longer than the radicle. TYPE SPECIES: *S. brasiliensis* Spreng. (Named in honor of Antonio Sebastiani, 1792-1831, Italian professor of botany.)

As circumscribed by Pax, a diversified genus of some 75 species, at least



three-quarters of which are native to southern Brazil. Although Pax enumerated three species from the Old World, one of these (*S. inopinata*, from Africa) has been made the type of a segregate genus *Duvigneaudia* by Léonard, primarily on the basis of its drupaceous fruit and ecarunculate seeds. Three species from Indonesia (two described by Van Steenis) are of dubious affinity, and their possible relationship to *Duvigneaudia* needs to be examined. *Sebastiania Chamaelea* (L.) Muell. Arg., an herb found across the tropical belt from Africa to northern Australia, appears to be fairly closely related to the weedy American herb, *S. corniculata* (Vahl) Muell. Arg., and there is no reason to question its position in the genus. *Sebastiania* consequently has at least one gerontogean representative, but its remarkable paucity of development there remains unexplained.

Our only species, *Sebastiania fruticosa* (Bartr.) Fern. (*S. ligustrina* (Michx.) Muell. Arg.), is a shrub 3–4 m. high which is found in hardwood forests (often along streams) from North Carolina to Florida, west to eastern Texas. The species is the only representative of sect. *STILLINGIOPSIS* (Muell. Arg.) Webster,<sup>22</sup> which differs from sect. *CNEMIDOSTACHYS* (Mart.) Webster<sup>23</sup> in its ovoid seeds, smooth ovary, connate male sepals, and woodier habit. It is much closer to sect. *SEBASTIANIA*, which differs only in its reduced male calyx lobes and larger bracteal glands; the type species, *S. brasiliensis*, strongly resembles *S. fruticosa* in many respects.

A peculiarity which is shared by some other Hippomaneae is that *Sebastiania fruticosa* does not produce noticeably milky juice, even though laticifers are present (according to Herbert). The single chromosome count,  $2n = 56$  (Perry), suggests that the species may be an octoploid on a base of seven. However, this report merits reinvestigation, since  $x = 7$  has not been confirmed for any other genus of Hippomaneae.

Certain Mexican species of *Sebastiania* have attained a degree of botanical notoriety as the source of "Mexican jumping beans" ("semillas brincadores"). The two plants most often cited in this connection are *S. Pringlei* Wats. and *S. Palmeri* Rose; Pax (under the latter species) has reviewed the literature, which is more voluminous than the apparent triviality of the phenomenon would seem to warrant. Within a few years after Hooker provided the first botanical description in 1854, the cause of the erratic behavior of *Sebastiania* seeds was shown to be due to the activity of the larva of a microlepidopteran moth (*Laspeyresia saltitans*, Tortricidae). Similar "springenden Bohnen" have also been reported from other taxa of Hippomaneae (e.g., *Colliguaya odorifera* Mol., *Sapium biloculare* (Wats.) Pax), and in all instances (where known) the causative agent has proved to be a tortricid larva. Although little has appeared in the literature since the plethora of papers between 1890 and 1926, a number of questions remain to be resolved. The biological relationship

<sup>22</sup> *Sebastiania* sect. *Stillingiopsis* (Muell. Arg.) Webster, comb. nov. *Gymnanthes* sect. *Stillingiopsis* Muell. Arg. *Linnaea* 32: 96. 1863.

<sup>23</sup> *Sebastiania* sect. *Cnemidostachys* (Mart.) Webster, comb. nov. *Stillingia* sect. *Cnemidostachys* (Mart.) Baill. *Étud. Gén. Euphorb.* 515. 1858. *Cnemidostachys* Mart. *Nov. Gen. Sp.* 1: 66. 1824.



between lepidopteran and plant has not been studied in sufficient detail (i.e., through entire life-cycles) and the classification of the taxa of both host and parasite is still imperfect. Mueller originally determined the infected Mexican plant as *Sebastiania Pavoniana* (Muell. Arg.) Muell. Arg., and it is possible that most of the various Mexican host plants may prove to be varieties of that species.

Generic limits in the tribe Hippomaneae have long been subject to controversy, and it is not certain that taxa such as *Sebastiania* can be maintained in their present circumscription when more data become available. Baillon, taking a broad view of generic limits, included *Sebastiania*, *Stillingia*, *Maprounea*, and *Sapium* within a very inclusive genus *Excoecaria*. Mueller separated *Excoecaria*, *Maprounea*, and *Sapium*, but kept *Sebastiania* united with *Gymnanthes*. Bentham, followed by Pax, separated *Gymnanthes* on the basis of its reduced perianth. There is little doubt that *Gymnanthes* and *Sebastiania* are closely related, but they can be fairly readily distinguished, so there seems to be no urgent necessity to combine them. The Old World genus *Excoecaria* is also closely related to *Sebastiania* but is sufficiently distinguishable by virtue of its axillary dioecious inflorescences and ecarunculate seeds.

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#### 18. *Gymnanthes* Swartz, Prodr. Veg. Ind. Occ. 95. 1788.

Glabrous trees or shrubs; sap not appreciably milky. Leaves alternate, stipulate, unlobed, entire or dentate; petiole short, not glandular. Plants monoecious [rarely dioecious]; inflorescences spiciform, axillary, protected by a conspicuous bud, bisexual; female flower usually only 1 per inflorescence; long-pedicellate from the lowermost node; male flowers



[1–]3 per cymule, occupying remaining nodes; bracts more or less glandular at base. Flowers apetalous; calyx small to absent; disc absent. Male flower: calyx rudimentary, of 1 or 2 small sepals often confounded with bractlets, or absent; stamens 2 or 3 in lateral flowers of the cymule, 3–5 in the central flower; filaments free or basally connate; pollen subglobose, tectate, tricolporate, circular or 3-lobed in polar view; rudimentary gynoecium absent. Female flower: calyx minute, of 2 or 3 reduced sepals [or absent]; carpels 3; styles free or connate at base, unlobed, slender and recurved; ovary smooth, stipitate [or sessile]; ovules 1 in each locule, anatropous. Fruit capsular; columella 3-winged, persistent. Seeds subglobose, smooth, dry, carunculate; cotyledons much broader than radicle. LECTOTYPE SPECIES: *G. lucida* Sw.; typification effected by Grisebach, Fl. Brit. W. Indian Is. 50. 1859. (Name from Greek, *gymnos*, naked, and *anthos*, referring to the highly reduced perianth of the flowers.) — CRAB-WOOD.

As circumscribed by Pax, a small genus of 12 species confined to the Caribbean region, mostly in the West Indies. *Gymnanthes* is extremely difficult to separate from *Actinostemon*, on the one hand, and from *Sebastiania*, on the other, and Baillon's suggestion to merge these and some other genera under *Excoecaria* is not entirely without merit. However, until additional data, such as chromosome counts (unrecorded for any species of *Gymnanthes*), are forthcoming, the traditional circumscription is diffidently maintained here.

Our only representative, *Gymnanthes lucida* Sw., the most widespread species in the genus, has been recorded from southern Florida throughout the Bahamas and Greater Antilles to Guadeloupe, in the Lesser Antilles. In Florida it is mainly confined to hammock vegetation on limestone in the Miami area and Florida Keys, extending to Key West; the northernmost collection known is from Palm Beach County. The species is easily distinguished from all its congeners by the remarkable stipitate ovary, the gynophore attaining a centimeter in length and appearing as a prolongation of the peduncle. The solitary, long-pedicellate female flower and stiff, crenate leaves also make it readily separable from *Sebastiania fruticosa*, even though the genera on the whole may be difficult to distinguish.

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Under family references see HERBERT, NOZERAN, PAX & HOFFMANN (1912, V: 81–88), and PUNT.

SARGENT, C. S. *Gymnanthes*. Silva N. Am. 7: 29–32. pl. 309. 1895.

#### 19. *Stillingia* Garden in Linnaeus, Mant. Pl. 19. 1767.

Glabrous herbs, shrubs, or small trees; sap not evidently milky. Leaves alternate [opposite, or verticillate]; stipules small and often glandular; blade unlobed, pinnately veined, [with or] without basal glands, serrate. Plants monoecious; inflorescences terminal, spiciform; female flower 1 per



bract, proximal; male flowers [1–]3 or more per bract, distal; bracts biglandular. Flowers apetalous, disc absent. Male flower: calyx 2-lobed, lobes imbricate; stamens 2, filaments connate below, anthers extrorse; pollen ellipsoid to spheroid, with [1] 3 colpi, tectate but sometimes pseudoreticulate, slightly to distinctly 3-lobed in polar view; rudimentary gynoeceum absent. Female flower: sepals 3, imbricate [sometimes absent]; carpels 3 [2]; styles more or less connate, unlobed, slender; ovary smooth (not muricate); ovules 1 in each locule, anatropous. Fruit capsular; columella dilated distally, often deciduous, surrounded by 3-horned structure (“gynobase”) left after dehiscence of the carpels. Seeds not or scarcely compressed, [smooth or] rugulose, the caruncle sunk in a ventral depression [absent in some taxa]; endosperm present; embryo straight, the cotyledons broader than the radicle, cordate at base. TYPE SPECIES: *S. sylvatica* Garden ex L. (Named in honor of Benjamin Stillingfleet, 1702–1771, English botanist and disciple of Linnaeus).

A well-defined genus of 26 or 27 known species with a strange distribution somewhat paralleling that of *Sebastiania*. The vast majority (23) of the species are American, but two or three occur in the Mascarene Islands and one is known only from Fiji. There seems to be no reason to question the assignment of these Old World species, which belong to the single sect. *PACHYCLADAE* Pax, to *Stillingia*.

The American species have been revised by Rogers, who has reaffirmed the distinctness of the genus. Rogers regards *Sapium* as the genus most closely related but differing in its united sepals, fleshy seed coat, usually elongated foliar glands, and especially in its lack of the three-horned “gynobase” which characterizes the dehiscent fruit of *Stillingia*.

The infrageneric taxa of *Stillingia* have been differently treated by the last two monographers, Pax dividing the genus into six sections, Rogers recognizing two subgenera with a total of five series. As construed here, *Stillingia* comprises four sections, two of which are represented in the United States. However, none of the southwestern representatives of sect. *LEPTOSTACHYAE* Pax (ser. *Treculianae* Rogers), which are characterized by reduced female calyx and ecarunculate seeds, enter our area.

Both species of *Stillingia* in the southeastern United States belong to sect. *STILLINGIA* by virtue of their well-developed female calyces and carunculate seeds. *Stillingia aquatica* Chapm., of ser. *OPPOSITIFOLIAE* Rogers, an erect shrub with lenticellate twigs, is confined to swampy areas in Florida, except for outlying stations in southwestern Georgia and Baldwin County, Alabama. Closely related, although placed in a different series, *SYLVATICA* Rogers, on account of its herbaceous nonlenticellate stems from an enlarged rootstock, is *S. sylvatica*, queen’s delight. This species, which is found from southeastern Virginia to Florida, westward into Kansas and New Mexico, occurs in our area mainly in dry habitats (e.g., sandy flats or pine woods) on the Coastal Plain. It is thus ecologically separated from *S. aquatica*, but Rogers has suggested that it hybridizes both with that species and, to the west, with *S. texana* I. M. Johnston.



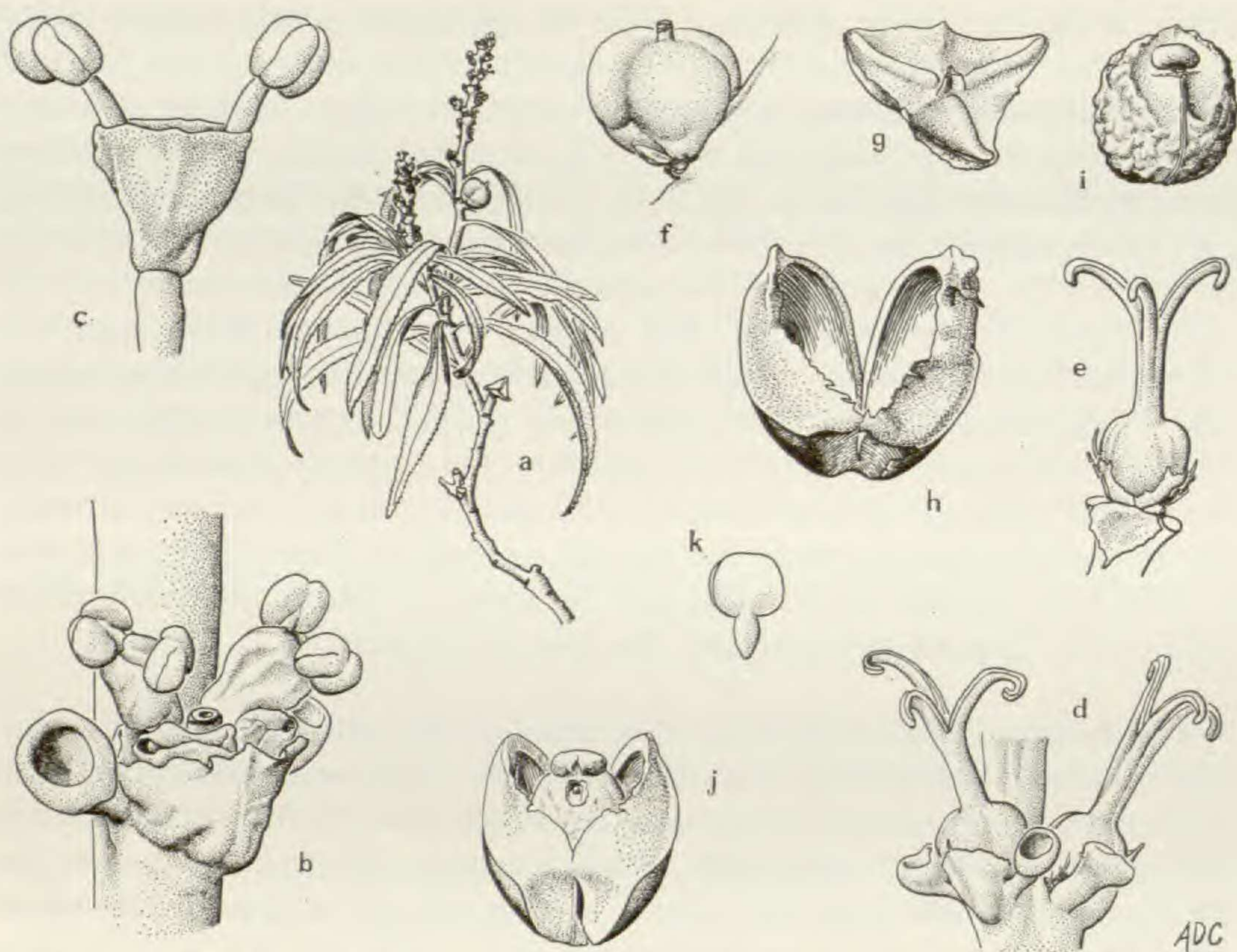


FIG. 5. *Stillingia*. a-i, *S. aquatica*: a, branchlet with male flowers and nearly mature fruit,  $\times \frac{1}{2}$ ; b, male cymule, showing bract, two cup-shaped glands, pedicel of central male flower, two male flowers at anthesis, two buds,  $\times 8$ ; c, male flower — note synsepalous calyx,  $\times 12$ ; d, two female flowers from base of inflorescence,  $\times 12$ ; e, female flower with glands removed and bract retracted to show two perianth segments,  $\times 6$ ; f, nearly mature schizocarp with persistent perianth segment at base,  $\times 2$ ; g, persistent base of schizocarp (cf. a, f) with lower part of brittle columella,  $\times 4$ ; h, segment of schizocarp wall,  $\times 4$ ; i, seed,  $\times 4$ . j, k, *S. sylvatica*: j, segment of schizocarp with seed,  $\times 2$ ; k, embryo,  $\times 2$ .

Identification of specimens from Florida, where *S. aquatica* and *S. sylvatica* are extensively sympatric, may therefore be difficult, but in addition to the difference in habit *S. sylvatica* may be recognized by its less distinctly petiolate leaves and its smooth and larger seeds (3–7 mm. broad vs. 2–3 mm. in *S. aquatica*). In extreme southern Florida (Dade County) occurs the form recognized by Small as *S. tenuis* and designated by Rogers as *S. sylvatica* ssp. *tenuis* (Small) Rogers. As Rogers suggests, it may be a narrow-leaved ecotype adapted to the limestone substrate in the Miami area. However, careful field studies throughout peninsular Florida are certainly needed in order to evaluate the status of this southernmost population as well as the putative hybrid swarms between *S. aquatica* and *S. sylvatica*. The evident close relationship between all these taxa suggests that *S. aquatica* and *S. sylvatica* should probably be placed in the same series.

As in the other Hippomaneae, almost nothing is known of the reproductive biology of the species of *Stillingia*, although the pollen structure and



conspicuous glandular bracts suggest that they are at least partly entomophilous. The chromosome number of *S. sylvatica* was reported to be  $2n = 36$  by Perry, but Rogers was unable to confirm this and thought that Perry's count was probably too low. The only firm count for any species of *Stillingia* appears to be  $2n = 60$  in *S. sanguinolenta* Muell. Arg., of ser. OPPOSITIFOLIAE. Until more taxa in this and related genera are studied, it will not be clear whether the basic number in that species is 10 or 15.

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#### 20. *Sapium* P. Browne, Civ. Nat. Hist. Jamaica 338. 1756.

Glabrous trees or shrubs; stems usually with copious milky latex. Leaves alternate, stipulate; petiole usually biglandular at apex; blade denticulate, pinnately veined. Plants monoecious [rarely dioecious]; flowers in terminal bisexual spikes; female flowers several per spike, solitary in the axil of each proximal bract; male flowers in several-flowered clusters in the axils of distal bracts; bracts conspicuously biglandular at base. Flowers apetalous, disc absent. Male flower: calyx synsepalous, 2- or 3-lobed, lobes imbricate or open at anthesis; stamens 2 or 3, filaments free or basally connate; anthers extrorse; pollen subglobose, tectate, tricolporate, 3-lobed in polar view; rudimentary gynoecium absent. Female flower: calyx lobes [2] 3–5, small; carpels [2] 3; styles [free or] connate, unlobed, slender; ovary smooth; ovules 1 in each locule, anatropous. Fruit capsular [sometimes subdrupaceous]; valves often somewhat woody; columella slender and usually persistent. Seeds rounded (not compressed), outer seed coat fleshy and pseudoarillate, ecarunculate; cotyledons broader than radicle. (Including *Triadica* Lour.) TYPE SPECIES: *S. aucuparium* Jacq.<sup>24</sup> (Classical name used by Pliny for a resin-exuding species of *Pinus*; ultimately derived from Celtic, *sap*, fat, perhaps alluding to the sticky latex.) — MILK-TREE.

A pantropical genus of over 100 species, the majority American, only one native to the United States. In terms of discrimination of species,

<sup>24</sup> As pointed out by Croizat (Jour. Arnold Arb. 24: 174. 1943), the Jamaican plant on which Browne based *Sapium* was later designated as *S. aucuparium* by Jacquin. Although Jacquin subsequently applied the name to a South American species, his original disposition must be followed. Consequently, *S. aucuparium* Jacq. is the correct name for the species treated in most floristic manuals as *S. jamaicense* Sw.; the plant generally called *S. aucuparium* probably should take the name *S. salicifolium* HBK.



*Sapium* is one of the most difficult genera in the Euphorbiaceae. Our comprehensive ignorance of the reproductive biology and ecology of the species makes it impossible at present to pinpoint where the difficulty lies. Hemsley's work, as far as it went, appears to be sound, and his illustrations at least provide a point of departure for further studies; but Pax's monograph is extremely difficult to use, and his supraspecific taxa are probably highly unnatural.

In the southeastern United States, *Sapium* is represented only by the naturalized *S. sebiferum* (L.) Roxb. (*Triadica sebifera* (L.) Small), Chinese tallow tree, which is commonly cultivated as an ornamental. Wild trees have been found in low, often swampy, areas in South Carolina, Georgia, and Louisiana. The species belongs to sect. TRIADICA (Lour.) Muell. Arg., a group of six Asiatic species characterized by having a somewhat fleshy fruit and by the seed coat being white and adherent to the columella, rather than reddish and free from the columella as in most tropical American species.

In the United States, *Sapium sebiferum* is grown mainly as an ornamental, especially for the foliage, which turns bright red in autumn. In central and southern China, Japan, and northern India, however, the tree is cultivated for the seeds. Both waxy seed coat and endosperm are used, the former providing the "tallow" used for candle-making in China, and the latter yielding an oil with some of the properties of tung oil. Unfortunately the labor costs involved in harvesting the fruits preclude commercial exploitation of the tree in countries such as the United States.

Small recorded a second species, *Sapium glandulosum* (L.) Morong, evidently on the basis of a Curtiss collection from near Pensacola, but the plant has not been re-collected and cannot be regarded as naturalized. The only other species of *Sapium* in the United States is *S. biloculare* (Wats.) Pax, one of the Mexican jumping-bean plants, which enters southern Arizona.

Perry has reported  $2n = 36$  in *Sapium sebiferum*, which is the only published chromosome number for the species. Ventura found that embryo-sac development was of the normal type in trees studied in Italy, but reported that only one seed developed per capsule; this is quite at variance with our plants, in which three seeds regularly develop in each fruit.

Although merged by Mueller with *Excoecaria*, *Sapium* has been recognized by most botanists on the basis of its monoecious inflorescence production, fleshy-coated seeds, and biglandular petioles. As pointed out by Pax, the relationship to *Stillingia* is probably closer, but Rogers has shown that *Sapium* can usually be distinguished from that genus by its fleshy seeds, elongated foliar glands, and lack of a persistent gynobase upon dehiscence of the fruit.

According to Horn and Polhamus, the rubber contained in latex of *Sapium* species is comparable in quality to the best *Hevea* rubber and, in fact, surpasses the latter in strength and elasticity. However, the trees are difficult to tap, and significant commercial production has never been



established. Because of the abundance of the plants in Latin America, it would appear that further investigation of the potentialities of *Sapium* latex might be warranted.

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21. **Hippomane** Linnaeus, *Sp. Pl.* 2: 1191. 1753; *Gen. Pl.* ed. 5. 499. 1754.

Glabrous trees or shrubs; milky latex copious, poisonous. Leaves alternate, stipulate (stipules caducous); petioles elongated, with a single gland at the apex; blade pinnately veined, more or less cordate. Plants monoecious [dioecious]; inflorescence spiciform, terminal, bisexual, the rachis more or less thickened; female flowers few, solitary at proximal nodes; male flowers several to numerous in dense glomerules at each of the distal nodes; bracts conspicuously biglandular at base. Flowers apetalous, disc absent. Male flower: calyx 2- or 3-lobed, lobes imbricate; stamens 2, filaments connate; anthers extrorse; pollen subglobose, tectate, 3-colporate, 3-angled in polar view; rudimentary gynoeceum absent. Female flower



sessile: calyx 3-parted; carpels (5) 6–9; styles connate at base, unlobed, spreading and recurved, densely papillate; ovary smooth; ovules 1 in each locule, anatropous. Fruit drupaceous, mimicking an apple, with yellowish or reddish fleshy exocarp, bony endocarp. Seeds not compressed, smooth, ecarunculate; endosperm present; cotyledons flat, much longer and broader than the radicle. LECTOTYPE SPECIES: *H. Mancinella* L.; see Baillon, Étude Gén. Euphorb. 540. 1858. (Name from Greek, *hippos*, horse, and *mania*, fury, referring to the effect of the poisonous latex.) — MANCHINEEL.

A small tropical American genus of two or three species, well characterized by the multilocular drupaceous fruit which is so apple-like in appearance that it has been the cause of serious poisonings. Two very closely related species with smaller drupes and spinose leaves, *H. spinosa* L. and *H. horrida* Urb. & Ekm., are endemic to dry scrub on limestone in southwestern Hispaniola. Our representative is the well-known manchineel tree, *Hippomane Mancinella* L.,  $n = 11$ ,<sup>25</sup> which is widespread along seashores in the Caribbean area from Florida to Mexico, Colombia, and Venezuela, with outlying populations in the Galapagos and Revillagigedo Islands. In Florida, the manchineel is restricted to the Keys and the immediately adjacent mainland, where it is found in hammock vegetation behind the mangrove zone.

From the earliest days of European colonization the manchineel has had a sinister reputation, and its toxicity has been exaggerated by some writers; still, there is no doubt that the latex is extremely dangerous if taken internally, and it can produce severe irritation of the skin. The wood has, in the past, been used here and there in the West Indies for making furniture, but this has now almost ceased, as the trees have been ruthlessly extirpated from many parts of their previous range.

Despite its widespread occurrence and familiarity, the reproductive biology of the manchineel remains almost completely unknown; but in our area it flowers in April. The pollination process and embryological development have not been followed, nor has germination and seedling establishment been carefully studied. The affinities of *Hippomane* have seldom been discussed, but there seems to be no reason to dissent from Baillon's opinion that it is very close to *Sapium*. The overall habit of the manchineel certainly recalls species of that genus, and it can scarcely be distinguished generically except on the basis of its indehiscent multilocular fruit.

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<sup>25</sup> Previously unpublished chromosome count by Dr. Jack Ellis, based on examination of meiosis in male flower buds of shrubs growing at Auchenskeoch Beach, Tobago (Webster et al. 9825).



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Tribe EUPHORBIEAE [Dumort.]

Subtribe Euphorbiinae Hurusawa

22. **Euphorbia** Linnaeus, Sp. Pl. 1: 450. 1753; Gen. Pl. ed. 5. 208. 1754.

Herbs, shrubs, or trees of diverse habit, aërial parts sometimes succulent, latex whitish. Leaves alternate, opposite, or whorled, persistent or deciduous (or sometimes caducous and then plants appearing leafless); stipules present or absent, sometimes represented by glands; blade undivided (sometimes lobed), usually pinnately veined, eglandular. Plants monoecious or rarely dioecious; inflorescence a bisexual (rarely unisexual) pseudanthium (cyathium); cyathia borne in terminal or axillary dichasia or pleiochasia (or, by reduction, apparently solitary). Cyathium with a solitary terminal female flower subtended by (4) 5 male cymes, the bracts opposite the male cymes fused into a radially or isobilaterally symmetrical, campanulate to hemispheric involucre; tips of bracts alternating with 4 or 5 (rarely fewer) glands (nectaries); glands entire, 2-lipped, or variously lobed, sometimes with petaloid appendages; male cymes monochasial or possibly dichasial at base, each developing 1–10 or more flowers; bracteoles of male monochasia conspicuous to reduced or absent, often fringed or lacerate, sometimes partly fused into the involucre partitions. Male flowers monandrous, simulating a single stamen; perianth usually absent, very rarely developed as a small cup (more commonly represented by an articulation); anthers dehiscing longitudinally and “introrsely” (i.e., centripetally); pollen subglobose, tricolporate, reticulate to tectate (psilate), sometimes operculate, with conspicuous intine thickenings parallel to colpi. Female flower pedicellate, pedicel often reflexed; perianth of 3–6 more or less united scalelike sepals or more commonly rudimentary or absent; carpels 3 (very rarely 2 or 4); styles free or basally connate, bifid or rarely entire; ovary glabrous or pubescent, often angled or carinate; ovules 1 in each locule, anatropous, with a more or less evident nucellar beak; embryo sac normal (Polygonum type) or rarely of various aberrant tetrasporic types. Fruit capsular [rarely drupaceous]; columella more or less persistent. Seeds smooth, ridged, or variously pitted or tuberculate, with or without a caruncle; endosperm copious; cotyledons fleshy, broader



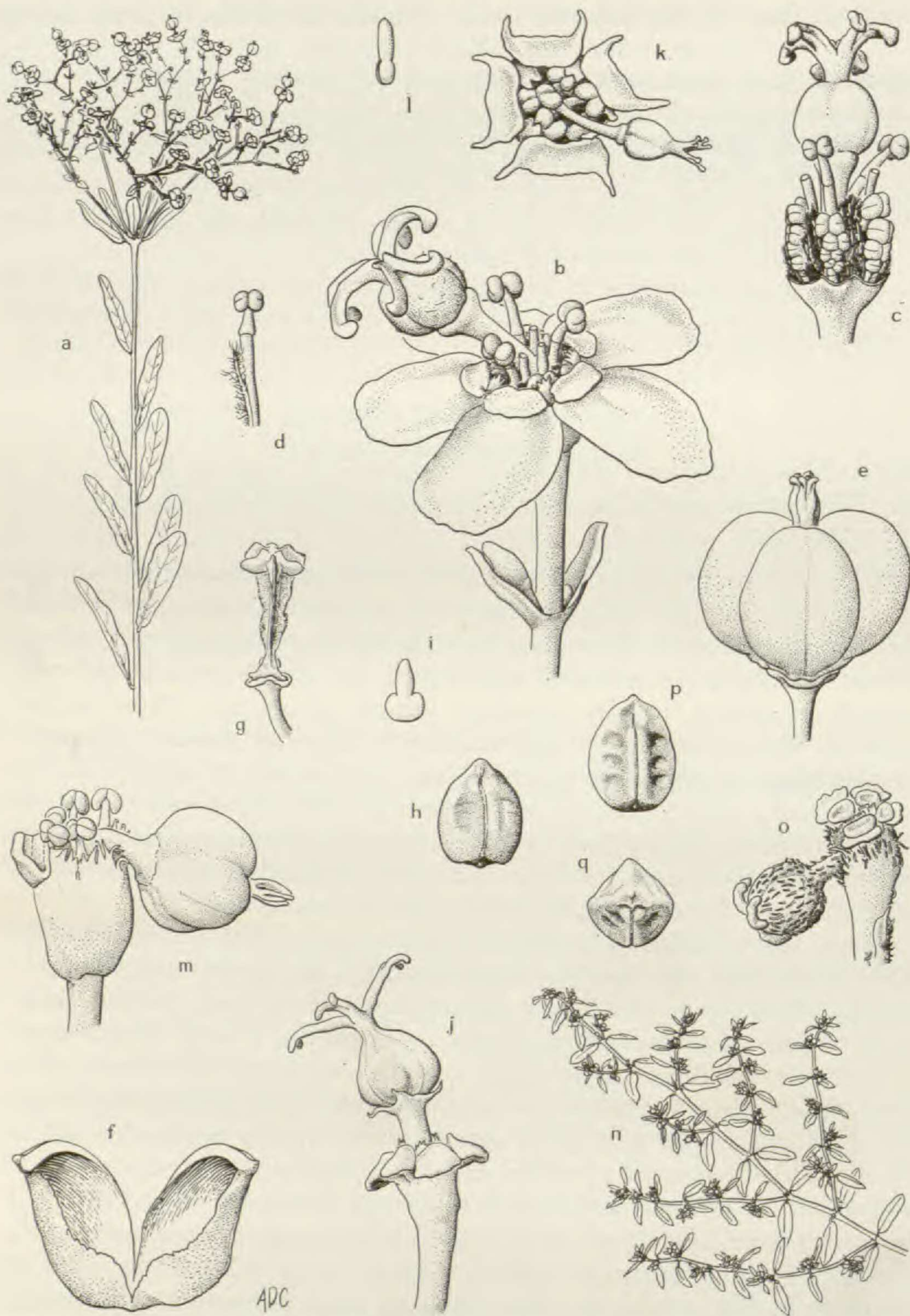


FIG. 6. *Euphorbia* and *Chamaesyce*. a-i, *Euphorbia corollata*: a, upper part of small plant,  $\times \frac{1}{2}$ ; b, cyathium,  $\times 8$ ; c, cyathium with walls removed to show cymules of male flowers and hairy bracteoles,  $\times 8$ ; d, male flower with bracteole—note articulation with pedicel,  $\times 8$ ; e, nearly mature schizocarp,  $\times 6$ ; f, segment of schizocarp, after dehiscence,  $\times 6$ ; g, columella of schizocarp,  $\times 6$ ; h, seed,  $\times 6$ ; i, embryo oriented as in seed,  $\times 6$ . j, *E. inundata*: cyathium and female flower with three-lobed perianth,  $\times 4$ . k, l, *E. commutata*: k, cyathium from above,  $\times 8$ ; l, embryo, oriented as in seed (compare with "i"),



than the radicle. (Including *Agaloma* Raf., *Dichrophyllum* Kl. & Garcke, *Elaeophorbia* Stapf, *Galarhoeus* Haw., *Poinsettia* Graham, *Tithymalopsis* Kl. & Garcke, *Tithymalus* J. Gaertn. [nom. cons.], and *Zygophyllidium* (Boiss.) Small.) LECTOTYPE SPECIES: *E. antiquorum* L.; see Millspaugh, Field Mus. Publ. Bot. 2: 306. 1909. (Named for Euphorbus, physician to King Juba of Numidia, a contemporary of Pliny, Euphorbus having drawn attention to the properties of the succulent *E. officinarum* vel aff.) — SPURGE.

In the broad circumscription of Pax & Hoffmann, *Euphorbia*, with over 1500 species, is the largest genus in the family and one of the largest among the angiosperms. This inclusive genus is characterized by its more or less regular bisexual pseudanthium, to which the term "cyathium" has been applied by most workers. Boissier, in the first general monograph, placed the cyathium-bearing Euphorbiaceae into only four genera: *Anthostema*, *Euphorbia*, *Synadenium*, and *Pedilanthus*. Among these, *Euphorbia* included all the species in which the male flower lacks a perianth and the cyathial involucre bears four or five glands. Pax & Hoffmann admitted a number of additional genera, such as *Stenadenium* and *Monadenium*, which differ from *Euphorbia* only in relatively slight modifications of the cyathium. The least justifiable segregation would appear to be the recognition of the genus *Elaeophorbia* Stapf for certain African species with drupaceous fruits; these species should be returned to *Euphorbia* subg. EUPHORBIA, where they find a place adjacent to sect. TEKEANAE Croizat.<sup>26</sup>

Croizat and Dressler, in a number of articles, have severely criticized the traditional circumscription of *Euphorbia* (without, however, using most of the segregate taxa in their own publications). Some of these criticisms have considerable merit, as the current concepts of generic limits in the Euphorbieae are indeed illogical and unnatural. The African genera *Monadenium* and *Synadenium*, although generally accepted by most 20th century workers, are evidently allied to *Euphorbia* sect. TIRUCALLI and are scarcely more distinctive overall than are many of Boissier's sections which are usually retained within *Euphorbia*.

If one accepts the position that the cyathium is a tribal character of the Euphorbieae rather than diagnostic for the genus *Euphorbia*, other criteria must be sought for generic delimitation in the tribe. The tremendous diversity in habit, leaf morphology, chromosome number, and pollen configuration might at first appear to favor the dissolution of *Euphorbia* into a number of smaller genera. However, a review of the

<sup>26</sup> *Euphorbia* sect. *Elaeophorbia* (Stapf) Webster, stat. nov. *Elaeophorbia* Stapf, Hooker's Ic. Pl. IX. 4: pl. 2823. 1906.

× 6. m, *E. dentata*: cyathium, × 8. n-q, *Chamaesyce maculata* (*C. supina*): n, part of prostrate plant to show branching habit, arrangement of leaves, and interpetiolar stipules, × 1/2; o, cyathium, × 16; p, q, seed, adaxial surface and from above, × 16.



taxonomic history of the Euphorbieae is sufficient to indicate that the problem does not have an obvious solution. Variations in such features as the cyathial glands (appendaged or not), seeds (carunculate or not), and female flowers (naked or "calyculate") do not seem to show strong correlation with major phyletic groups. There is the additional practical difficulty that the numerous exceptions to such characteristics (e.g., carunculate seeds) make it extremely difficult to find good "key" characters to diagnose segregate taxa. If the various microgenera of Euphorbieae cannot be easily distinguished, there seems little reason to adopt them simply because they represent evolutionary units; it is quite as easy to discuss the evolution of these taxa if they are referred to as infrageneric components of *Euphorbia*.

The present author finds himself no more able to resolve this taxonomic impasse than have the many others who studied the situation earlier. A major difficulty appears to reside in the lack of basic morphological and cytological data. Although many papers have been published on *Euphorbia*, most have dealt either with species in subg. ESULA or with the African succulents. Chromosome numbers are available for over 80 species, but many of these require confirmation, and no counts have been reported for *any* species in 18 of the 27 sections recognized by Boissier. Although much (perhaps too much!) has been published on the morphology of the cyathium, anatomical data — even for the cyathia — are inadequate for comparisons between sections, and the nature of the spines in the succulent taxa is still controversial. In view of this present scarcity of systematically meaningful facts, and in the face of the highly contradictory opinions of experts living and dead, a compromise view on generic limits is adopted in the present treatment: *Chamaesyce* is accepted confidently as a distinct genus, whereas all other segregate taxa, including *Poinsettia*, are relegated to subgeneric status within *Euphorbia*. This disposition is frankly one of expediency and does not claim either logical or phylogenetic justification. *Chamaesyce* happens to be a large and doubtless natural group of several hundred species which is rather easily definable. It seems more convenient, in practice, to recognize *Chamaesyce* as an independent genus than to retain it within *Euphorbia*; whereas, in my opinion, this is not true, in our present state of knowledge, for the other taxa of Euphorbieae in question.

As thus delimited, *Euphorbia*, *sensu stricto*, is still a large, polymorphic genus consisting of more than 1000 species distributed into about seven subgenera; in the southeastern United States it is represented by about 30 native or naturalized species belonging to four subgenera. All species of three other subgenera recognized by Wheeler (EREMOPHYTON, LYCIOPSIS, and RHIZANTHIUM) are confined to the Old World and in our area will be found only in cultivation.

Subgenus ESULA Pers. (§ *Tithymalus*, of Boissier), with over 500 species, is probably the largest and most diversified group within *Euphorbia*; it includes some of the most primitive as well as most highly specialized taxa in the genus. Despite this remarkable amplitude of diversifica-



tion, the great majority of taxa of subg. ESULA have in common alternate phyllotaxy (at least below), exstipulate leaves, and bibracteate cyathia with exappendiculate glands. Boissier's treatment of this group in De Candolle's *Prodromus* is unsatisfactory as regards supraspecific categories, since he crowded over 300 species into a single one of his 27 sections. Prokhanov, in Flora URSS, has tended toward the other extreme in recognizing ten sections and a large number of subsections and series for the relatively limited diversity of taxa found in the Soviet Union. In the present circumscription, the 17 Southeastern species of subg. ESULA are referred to three sections.

Section LATHYRIS Godron (§ *Epurga* Prokh.) includes only *Euphorbia Lathyris* L., a European species occurring as a weed (perhaps partially escaped from herb gardens). The species differs sharply from other representatives of subg. ESULA in its decussate phyllotaxy; thick-walled, tardily dehiscent capsules; and large (4–5 mm. long), roughened, carunculate seeds. Although it was placed at the opposite end of subg. ESULA in Boissier's arrangement, the group closest to sect. LATHYRIS would appear to be sect. MYRSINITEAE (Boiss.) Pojero, a group of Mediterranean perennial species with similar cyathia (horns of glands dilated, male bracteoles reduced). Our remaining species, which have the leaves alternate (at least below) and less massive capsules with smaller seeds, are about equally divided between two sections (very perceptively distinguished by Roeper in 1824, although without distinguishing names).

Section ESULA [(Roeper) Koch] includes those species of subg. ESULA with truncate to crenulate or bicornate nectaries, linear to oblong cotyledons, smooth ovaries, and prevailingly entire cauline leaves. Over 200 species have been described, primarily from temperate regions of the Northern Hemisphere, but extending into tropical latitudes along high mountain ranges. The section is close to sect. TITHYMALUS and not always easily distinguishable from it, but the placement of most individual species is usually not in doubt. Perhaps the local species of most dubious relationship is *Euphorbia trichotoma* HBK., a West Indian coastal plant which occurs in southern peninsular Florida as far north as Tampa Bay. Norton appears to have been correct in transferring it from sect. TITHYMALUS, and it seems best regarded as our only representative of subsect. PARALIOIDEAE Prokh., diverging from other taxa in the section by its crenulate leaves and peculiar branching pattern. There is a rather striking resemblance between *E. trichotoma* and *E. Paralias* L., a Mediterranean plant of similar maritime habitats, and the two may perhaps be vicariants.

Subsection ESULAE Boiss., a primarily Old World group of perennials with smooth, carunculate seeds, is represented in our area only by the pernicious introduced weed *Euphorbia Cyparissias* L.,  $2n = 20, 40$ ; other related species (e.g., *E. Esula* L.) have been introduced into the northern United States and Canada and may eventually be found in mountainous areas of the Southeast.

Subsection FOVEOSPERMAE Hurusawa, comprising Holarctic annuals or short-lived perennials with pitted, usually carunculate seeds, includes the



remaining five or six species in our area. Both exotic weeds, such as the ubiquitous *Euphorbia Peplus* L., and native species, such as *E. commutata* Engelm., are represented.

Section TITHYMALUS Roeper, characterized by rounded, entire cyathial glands; suborbicular cotyledons; and usually smooth seeds, includes at least 150 species, mainly of north temperate regions but with perhaps a majority in Eurasia. Our species fall into three subsections. The type species of the section, *Euphorbia Helioscopia* L., is an introduced European weed belonging to subsect. GALARRHAEI Boiss., a group of about ten species including annuals or biennials with obovate serrulate leaves and carunculate reticulately ornamented seeds. Our only native species, the rather variable *E. spathulata* Lam. (*E. dictyosperma* Fisch. & Mey.) differs from *E. Helioscopia* in having verrucose, rather than smooth, capsules.

Subsection PURPURATAE Prokh., a group of perennial rhizomatous species with generally entire leaves and roughened ovaries and seeds, is primarily Eurasian. Its only typical representative in North America is the taxonomically rather isolated *Euphorbia purpurea* (Raf.) Fern. (*E. Darlingtonii* Gray). Two additional species in our area, *E. platyphylla* L. and *E. obtusata* Pursh, are anomalous in their annual habit, and *E. obtusata* is somewhat transitional to subsect. GALARRHAEI in its serrulate leaves and slightly wrinkled seeds.

Subsection INUNDATAE Webster,<sup>27</sup> an entirely New World group, is represented in the Southeast by three related Coastal Plain species: *E. floridana* Chapm., *E. inundata* Torr., and *E. telephioides* Chapm. These plants resemble *E. Ipecacuanhae* in their habit and female flowers with perianth, but they differ in lacking stipules and appendages on the cyathial glands. It would appear that subsect. INUNDATAE is a group transitional in certain respects between subg. ESULA and subg. AGALOMA. Boissier included a dozen South American species in the same subsection, but further study is needed to determine whether these should be closely associated with the species of the United States.

Subgenus AGALOMA (Raf.) House, in the circumscription of Wheeler, is an American group of ten sections with approximately 100 species. Although plants of very diverse habit are included, the subgenus can be characterized by the appendiculate glands of the cyathium; the majority of species also have stipulate leaves and ecarunculate seeds. Boissier's treatment of the taxa now gathered into subg. AGALOMA is not very satisfactory, as his ten sections (II–XI) are not very well defined and are really equivalent to his subsections in sect. TITHYMALUS; doubtless they

<sup>27</sup> *Euphorbia* sect. *Tithymalus* subsect. **Inundatae** Webster, subsect. nov., foliis infra sparsis, stipulis nullis, capsulis calyculatis, seminibus ecarunculatis. **TYPUS:** *E. inundata* Torr.

Norton (Missouri Bot. Gard. Rep. 11: 2. 1899) pointed out that *Euphorbia Ipecacuanhae* L. must be transferred from subg. ESULA to subg. AGALOMA. Since *E. Ipecacuanhae* is by inference the type of Boissier's subsect. IPECACUANHAE, its excision necessitates renaming the residue of the taxon.



will be drastically recast in the next monographic revision. Three sections with about 10–12 species occur in the Southeast.

Section TITHYMALOPSIS (Kl. & Garcke) Boiss., typified by *Euphorbia corollata* L., is a taxonomically difficult and phylogenetically interesting group of rather uncertain limits. The typical element of the section may be referred to subsect. COROLLATAE Webster,<sup>28</sup> which includes perennial plants with rhizomatous or somewhat tuberous rootstocks, alternate exstipulate leaves below the inflorescence branches, five distinctly appendiculate cyathial glands, and finely or shallowly pitted seeds. Small recognized no less than ten binomials in the *E. corollata* complex, but the number of distinct species is surely less than that. *Euphorbia corollata* itself is a notoriously variable species, and some of the Smallian taxa (such as *Tithymalopsis apocynifolia* and *T. olivacea*) may prove to be tenable at subspecific rank when the variations are worked out. Species which appear distinct from *E. corollata* include *E. Mercurialina* Michx., with the lower leaves reduced to scales and an aspect resembling that of *E. Ipecacuanhae*; *E. Curtisii* Engelm., with very slender branching stems and narrow leaves; and *E. polyphylla* Engelm., with narrow revolute leaves and a habit recalling that of *E. Cyparissias*. Proposed species such as *E. discoidalis* Chapm., *Tithymalopsis exserta* Small, and *T. eriogonoides* Small, require further scrutiny before their status and relationships are clear. Extralimital species in Texas and Mexico, such as *E. Maysillesii* McVaugh, *E. sphaerorrhiza* Benth., and *E. Wrightii* Torr. & Gray, appear to belong to subsect. COROLLATAE on the basis of technical characters, but have a different aspect and may eventually have to be placed in a separate subsection.

Subsection IPECACUANHAE Boiss.,<sup>29</sup> which, in contrast to the preceding subsection, appears to be confined strictly to the United States east of the Mississippi River, includes plants the relationships of which have long appeared problematical. Boissier placed *Euphorbia Ipecacuanhae* in a subsection of subg. ESULA because of its presumably exappendiculate glands, but he noted its resemblance to *E. corollata*. As pointed out by Norton, however, *E. Ipecacuanhae* must be expelled from subg. ESULA because of its minutely stipulate leaves and its appendiculate cyathial glands; the appendages, though very narrow, are comparable to those in subg. AGALOMA. Although the distinct female perianth (Boissier's "caly-

<sup>28</sup> *Euphorbia* sect. *Tithymalopsis* subsect. **Corollatae** Webster, subsect. nov., ab subsect. IPECACUANHAE differt stipulis nullis, glandulis involucrorum 5, manifeste appendiculatis, capsulis ecalyculatis. TYPUS: *E. corollata* L.

<sup>29</sup> *Euphorbia* subsect. IPECACUANHAE Boiss. (DC. Prodr. 15(2): 101. 1862), implicitly typified by *E. Ipecacuanhae* L., is here restricted to that species and its near relatives and at the same time is transferred from subg. ESULA to subg. AGALOMA. The remainder of the species in Boissier's subsection remain in subg. ESULA as subsect. INUNDATAE Webster of sect. TITHYMALUS (see previous footnote). The species of sect. TITHYMALOPSIS may therefore be referred to three subsections: COROLLATAE, IPECACUANHAE, and subsect. **Innocuae** Webster, subsect. nov.: perennis, caulibus prostratis; foliis sessilibus, inferne sparsis, superne oppositis; cyathiis solitariis, glandulis 4 appendiculatis; seminibus scrobiculatis. TYPUS: *E. innocua* L. C. Wheeler.



culus") of *E. Ipecacuanhae* does suggest affinity to *E. inundata* and related species in subg. ESULA, the preponderance of characters (particularly the cyathial appendages, the leaf morphology, and the shallowly pitted seeds) argues for inclusion of *E. Ipecacuanhae* in sect. TITHYMALOPSIS. Subsection IPECACUANHAE, as redefined, then includes *E. Ipecacuanhae*, *E. gracilior*, Cronq., and some dubious populations which have been named *E. arundelana* Bartlett and *E. marilandica* Greene. It seems probable, as suggested by Gleason (New Britt. Brown Illus. Fl. Northeast. U. S. 2: 486. 1952), that these latter taxa represent hybrid swarms between *E. corollata* and *E. Ipecacuanhae*, but the necessary field and experimental studies to substantiate this hypothesis have not yet been made.

Section ZYGOPHYLLIDIUM Boiss., evidently related to sect. TITHYMALOPSIS but differing in habit (plants annual and more highly branched) and having tuberculate rather than pitted seeds, is a small North American group of perhaps six species. Only *Euphorbia hexagona* Nutt. ex Spreng. crosses into our area in Arkansas. It differs from all our taxa of sect. TITHYMALOPSIS in its prevailing unisexual cyathia with thickened acute glandular appendages, as well as in its completely different aspect. However, some western species of sect. TITHYMALOPSIS, notably *E. Wrightii*, show a strong resemblance to *E. hexagona*, except in having a thickened perennial root. Since Boissier's treatment, additional species more or less referable to sect. ZYGOPHYLLIDIUM have been described from Mexico, and it seems likely that the sectional boundaries will have to be redefined.

Section PETALOMA Boiss. is a North American group of three species, two of which enter our area in Arkansas and Louisiana. Plants of this section are easily recognizable by the annual root, sparingly branched stems with alternate leaves below, and conspicuously white-edged floral bracts subtending the large cyathia. *Euphorbia marginata* Pursh, the familiar snow-on-the-mountain, native to Texas, is cultivated in many southern gardens and may be found as an escape here and there, but has not yet been recorded as native to our area. Very similar, but differing in its narrower leaves and more densely pubescent capsule, is *E. bicolor* Engelm. & Gray, which enters Arkansas from Oklahoma and Texas. A third closely related species, *E. torrida* DC., is known from Mexico (San Luis Potosí, Veracruz, Campeche, and Oaxaca).

Subgenus POINSETTIA (Graham) House is an American taxon treated by Dressler as an independent genus with eleven species. The group is characterized by its reduced number of more or less cup-shaped exappendiculate glands (mostly one or two, rarely three or four), condensed dichasial or pleiochasial inflorescences, and tuberculate seeds. However, as Dressler himself pointed out, the poinsettias show a strong resemblance to taxa of subg. AGALOMA, especially species of sect. DICHILIUM Boiss. such as *Euphorbia lancifolia* Schlecht. Although the cultivated poinsettia, *E. pulcherrima* Willd. ex Kl., certainly appears to be very different from familiar representatives of subg. AGALOMA such as *E. corollata*, the genus *Poinsettia* as defined by Dressler is actually not as sharply defined as some sections within AGALOMA. Whether treated as genus or subgenus, its rela-



tionships with sect. *DICHILIUM* and other taxa within subg. *AGALOMA* need to be further evaluated.

In our area four native or naturalized species of subg. *POINSETTIA* have been recorded. Dressler has untangled much of the confusion surrounding these common weedy annuals, and it is apparent from his discussion that identifications in the literature are highly untrustworthy. The most widespread species in North America appears to be *Euphorbia dentata* Michx. (*Poinsettia dentata* (Michx.) Kl. & Garcke),  $2n = 14, 28, 56$ , which occurs over most of eastern temperate United States and extends south into Texas and Mexico. It may be recognized by its opposite, coarsely dentate leaves; floral leaves lacking basal red splotches; slender cyathium with bilabiate gland; and rounded, sharply tuberculate, usually carunculate seeds. Also widespread in eastern temperate North America and probably occurring throughout our area is *E. cyathophora* Murr. (*P. cyathophora* (Murr.) Kl. & Garcke),  $2n = 28, 56$ , a highly variable species which has suffered much confusion in taxonomic treatments. It may usually be recognized by having the lower leaves alternate; floral bracts red splotched; cyathia broader, with a larger gland; and finely tuberculate seeds without a caruncle. This species has been confused in many floristic manuals with *E. heterophylla* L. (*P. heterophylla* (L.) Kl. & Garcke), but, as shown by Dressler, that name is properly applied to a species of primarily tropical distribution which within our area has been found only in Louisiana and Florida. Although superficially resembling some forms of *E. cyathophora*, with which it is sympatric in much of the Caribbean region, *E. heterophylla* differs in its floral bracts lacking basal red splotches; its more slender cyathia with a round, stipitate gland; and its angular, more coarsely tuberculate seeds.

Burch, in a brief review of the Florida taxa of subg. *POINSETTIA*, has upheld *Euphorbia pinetorum* (Small) Webster<sup>30</sup> as a species distinct from *E. cyathophora* (to which Dressler had referred it as a synonym). Although it closely resembles certain narrow-leaved forms of *E. cyathophora* in aspect, it differs in having a perennial base with thickened storage roots and cyathia mostly with three or four glands. According to Burch, *E. pinetorum* is endemic to the pinelands on limestone in extreme southern Florida (Dade and Monroe counties).

The morphological patterns in many species of subg. *POINSETTIA* display a remarkable amplitude of variation; this is especially true of *Euphorbia cyathophora*, in which plants with linear and with pandurate leaves may be found intermingled in the same population. Some of the variation is doubtless ecotypic, and some may be due to hybridization. Dressler has suggested that introgression occurs between *E. dentata* and *E. heterophylla*, and the Florida populations of these two species would repay closer study. Curiously, no evidence of crossing between *E. dentata* and *E. cyathophora* has been reported, although these species are sympatric over hundreds of thousands of square miles.

✓<sup>30</sup> *Euphorbia pinetorum* (Small) Webster, comb. nov. *Poinsettia pinetorum* Small, Fl. Miami 111, 200. 1913.



Cytologically, the taxa of subg. *POINSETTIA* are interesting in that polyploid series ( $2n = 28, 56$ ) occur in at least *Euphorbia cyathophora* and *E. dentata*. Dressler suggested that the basic number of *Poinsettia* may be  $n = 14$ , but the reports of  $n = 7$  in one population of *E. dentata*, and the multivalent associations in *E. pulcherrima* described by Ewart & Walker would seem to point toward a basic number of  $n = 7$ . In contrast, *E. heterophylla* has proved to be uniformly tetraploid ( $2n = 28$ ), on the basis of counts from at least seven populations. It is evident that additional field surveys of chromosome number, when correlated with analysis of morphological variation patterns, may provide a fascinating insight into the dynamics of speciation in this group.

The commonly cultivated Christmas poinsettia, *Euphorbia pulcherrima* Willd. ex Kl.<sup>31</sup> (*Poinsettia pulcherrima* (Willd. ex Kl.) Graham) is grown in many parts of our area and may occasionally be found escaped in southern Florida, although it shows no signs of becoming naturalized. According to Dressler, the species is native to rocky canyons along the Pacific coast of Mexico, where it occurs in the tropical deciduous forest formation. In addition to its woody habit, it differs from our local representatives in its larger cyathia and seeds and glabrous stems.

Subgenus *EUPHORBIA*, a large group of some 400 Old World (mainly African) succulent species, includes most of the familiar "cactiform" euphorbias.<sup>32</sup> A single species, *Euphorbia lactea* Haw., has been reported as escaped from hedgerows in extreme southern Florida. According to Croizat, *E. lactea* is native to Ceylon, whence it was early introduced by the Dutch into cultivation on various West Indian Islands and eventually into Florida. Apparently the plant does not flower commonly in Florida, if at all, so that its spread must be entirely vegetative. Various other succulent species of subg. *EUPHORBIA* are cultivated in gardens in the Miami area. Perhaps the commonest is *Euphorbia Tirucalli* L., of sect. *APHYLLIS* Webb & Berth. (§ *Tirucalli*, of Boissier). It is a tree with slender, green, pencil-thick twigs bearing alternate deciduous leaves (and hence often appearing leafless); the latex is resinous and said to be poisonous to the touch, causing blindness if gotten into the eyes. Possibly the most familiar of the cultivated shrubby species of *Euphorbia* is *E. Milii* Desmoul. (*E. splendens* Boj.), the crown of thorns, which has stipular spines, well-developed leaves, and conspicuous red cyathial bracts. Although placed in sect. *EUPHORBIA* (§ *Diacanthium*) by Boissier, it appears to belong rather in sect. *GONIOSTEMA* along with a number of other Madagascar species characterized by spinose or comblike stipules, long peduncles, and variously colored cyathial bracts.

<sup>31</sup> Dressler deserves the commendation of horticulturalists who may prefer to recognize *Poinsettia* as a genus for salvaging the name *Poinsettia pulcherrima*; by describing a new Mexican species as *P. coccinea* Dressler, he thereby pre-empted an earlier epithet (*Pleuradena coccinea* Raf.) for the common ornamental species.

<sup>32</sup> In the narrowest possible generic circumscription within the Euphorbieae, the name *Euphorbia* would be restricted to a group of about 80 African and Asian succulents with ribbed stems and paired "stipular" spines (i.e., approximately to sect. *DIACANTHIUM* of Boissier, excluding *E. Milii* and *E. Bojeri*).



The relationships of subg. EUPHORBIA are controversial, but fortunately a resolution of the problem is beyond the scope of the present treatment. A few American species, such as *Euphorbia alata*, from Jamaica, and *E. phosphorea* Mart., from Brazil, could be referred to subg. EUPHORBIA on the basis of general habit; but it is possible, if not probable, that their resemblance to the African cactiform taxa is due to convergence, rather than consanguinity. The origin of subg. EUPHORBIA is, in any event, probably to be sought within subg. ESULA, where thick-stemmed species of sect. BALSAMIS Webb & Berth. (subsect. *Pachycladae*, of Boissier) suggest a starting point for the evolution in the direction of progressive succulence which reaches a climax in the *Cereus*-like taxa of South Africa.

Relationships within subg. EUPHORBIA are perhaps less well understood than in any other part of the genus, despite the relatively great degree of attention these succulent species have received. Boissier grouped most of the succulent and semisucculent species into five sections (XVIII–XXII) which, on the whole, are poorly defined. These fall into three main groups: (1) sects. EUPHORBIA (§ *Diacanthium*, of Boissier) and GONIOS-TEMA, with spines or crests of presumably stipular origin; (2) sect. ANTHACANTHA Lem. (§ *Euphorbium*, of Boissier), with spines (where present) of peduncular origin; and (3) sect. APHYLLIS Webb & Berth. (§ *Tirucalli*, of Boissier) with well-developed leaves and spineless stems, the plants scarcely differing from subsect. PACHYCLADAE of Boissier's sect. TITHYMALUS except in the succulence of their stems. Wheeler has associated Boissier's sects. CAULANTHIUM and RHIZANTHIUM into an additional succulent subgenus RHIZANTHIUM, but the reasons for this disposition are not quite clear, since the species included have in common mainly a thickened underground rootstock, but differ otherwise in reproductive characters and geographic distribution. It is quite possible that the various taxa of succulent euphorbias have been polyphyletically derived from different nonsucculent ancestors; the neotropical and paleotropical taxa almost certainly have separate origins. Since neither a satisfactory outline of supraspecific taxa nor a plausible phylogenetic scheme has yet been proposed, it is obvious that the succulent euphorbias present an especially fascinating challenge for future studies.

Morphological studies of the Euphorbieae have suffered from an excessive preoccupation by morphologists with homologies of the cyathium, aggravated by a lack of sufficient familiarity with the taxonomic diversity. The initial basic monograph of Roeper, in which morphological data were carefully related to classification, is an inspiring model which has never been sufficiently followed up, even for any major section within the genus.

The morphology and anatomy of the cyathium have been exhaustively studied by several generations of botanists since Roeper's day, and the basic structure is now rather well understood, although this knowledge has never been very effectively related to problems of generic and subgeneric delimitation in the Euphorbieae. The original thesis of Linnaeus that the cyathium is a hermaphroditic flower was still held a century later by Baillon and Payer, but Lamarck and A. L. de Jussieu had already



suggested (1788–1789) that it might be an inflorescence, and this was convincingly verified by Robert Brown, in 1818, and by Roeper, in 1824. For most of the past century the controversy with regard to the cyathium has shifted to questions of homologies between cyathial structures and the less modified reproductive organs of other Euphorbiaceae. Roeper suggested that the involucre of the cyathium represents a verticil of five connate bracts (such as may be seen in *Euphorbia Helioscopia* subtending the main rays of the umbelliform pleiochasium) and that the glands (nectaries) are duplex commisural structures of stipular origin. The glands, being formed by the fusion of adjacent glandular bracteal stipules, in this interpretation are thus homologous with the connate interpetiolar stipules of species of *Chamaesyce*. Unfortunately such a straightforward explanation has apparently seemed distasteful to many botanists with restless imaginations, and a number of alternative theories have been proposed, especially with regard to the origin of the glands. Haber, for example, after laborious scrutiny of microtome sections of cyathia, ignored the obvious evidence of gross morphology and interpreted the gland as representing “a pair of modified secondary branches of a lateral inflorescence branch, fused with which are parts of the adjacent involucre bracts.” Bodmann came to somewhat similar conclusions on the basis of an analysis of teratological cyathia, and proposed that the glands are really modified staminate flowers; but Neville more recently has supported the “classical” theory on the basis of other teratological specimens. It would appear that teratological evidence is equivocal, at best, and certainly cannot offer a convincing refutation of the “stipular” theory.

There seems to be no reason to discredit the Brown-Roeper theory of cyathial structure, but this does not mean that the problems are all “solved,” for a number of fascinating questions remain. There is a considerable gap between the primitive cyathium of *Anthostema* and that of the various genera of Euphorbiinae, and it is not apparent which, if any, of the cyathia of existing taxa should be regarded as most “primitive.” One curious feature, for example, is that the cyathia of the more primitive genera of Euphorbieae tend to be mostly four-merous, whereas those of the Euphorbiinae are commonly five-merous. The nature of the male “bracteoles” and partitions is still not entirely clear, and the evolution of the involucre nectaries also requires considerably more study. Presumably, appendiculate nectaries have been derived from unappendaged ones, judging from the condition in *Anthostema* and those species of *Euphorbia* with an evolute female calyx; but nectary appendages can be lost and a secondarily exappendiculate condition attained (e.g., in subg. POINSETTIA and in *Chamaesyce*). In species such as *E. Ipecacuanhae*, which stands on the borderline between subg. ESULA and subg. AGALOMA, it is far from clear whether the nearly exappendiculate condition is primary or secondary.

Except for the relative development of the calyx, the female portion of the cyathium is very stereotyped in all Euphorbieae, there always being a single terminal female flower (the apparent lateral position in *An-*



*thostema* seemingly due to differential growth). The main exception involves species with a tendency to unisexual cyathia, in which the female flower is reduced to a vestigial structure or is even entirely absent. Roeper pointed out that the first cyathium terminating the axis (in species of subg. *ESULA*) is often male, whereas cyathia on ultimate branches are either hermaphroditic or female. This initial production of male cyathia followed by hermaphroditic ones may be seen in many taxa of Euphorbiaeae, including the succulent species of subg. *EUPHORBIA* and subg. *POINSETTIA*.

A minor and perhaps unimportant controversy has surrounded the questions of the basic structure of the male part of the cyathium. The classic explanation espoused by Wydler (1843) envisioned the male flowers as borne in five monochasia (cincinni), the "paleae" within the cyathium being the modified bracteoles of the individual male flowers. Schmidt & Haber proposed a modification in which each male partial-inflorescence is regarded as a once-branched dichasium with a pair of monochasial branches. Schoute has judiciously considered this theory and rejected it as unconvincing; and, in fact, the male cymes of *Euphorbia* are usually so highly reduced that definitive proof may be impossible, making extended discussion of the problem profitless. An interesting analysis of the male inflorescence pattern was presented by Mansfeld in his description of *E. Tessmannii* Mansf., of sect. *ADENORIMA* (Raf.) Webster.<sup>33</sup> The cyathia of this plant have a pair of conspicuous bracts subtending the two male flowers of each cyme, and thus closely approach the Australian *E. paucifolia* (§ *CALYCOPEPLUS* (Planch.) Boiss.), except that the latter has four-merous rather than five-merous cyathia. It seems likely that the typical euphorbian cyathium, with the involucre partially divided by five partitions at the base, may be derived from these less highly modified cyathia in sect. *ADENORIMA* by fusion of the major male bract-pair, together, perhaps, with some of the bracteoles associated with flowers at distal forks of the monochasia.

The floral biology of *Euphorbia* is still rather poorly known, despite a considerable number of scattered observations. Many European species of subg. *ESULA* are pollinated primarily by flies (especially Muscidae, Syrphidae), but visits from a variety of other insects (small bees, beetles, etc.) have also been commonly recorded. In most species hermaphroditic cyathia are distinctly proterogynous, but since the first one or few cyathia produced in the inflorescence are often entirely male (e.g., in *E. Cyparissias*, *E. Peplus*, and *E. platyphylla*), the plant as a whole may be proterandrous. Gramuglio reports that over 70 per cent of plants of *E. dendroides* examined in Sicily had both the primary terminal cyathium and the first cyathia of the branches entirely male. Autogamy has been reported for *E. Peplus* (which may account for its success as a greenhouse weed) and probably occurs in other annual species as well.

<sup>33</sup>*Euphorbia* sect. *Adenorima* (Raf.) Webster, stat. nov. *Adenorima* Raf. Fl. Tellur. 4: 112. 1838. *Typus*: *E. punicea* Sw.



In view of the relatively unspecialized pollination mechanism in *Euphorbia*, it is rather surprising that so few hybrids have been reported. Most of the recorded instances involve European species of sect. ESULA, especially *E. Cyparissias*, *E. Esula*, *E. lucida*, and *E. virgata* (Zimmermann); and it is interesting that no crosses have been reported between species in sect. TITHYMALUS and sect. ESULA. During the 20th century, some of these European weeds have been introduced into North America, and Moore has reported on the situation in Canada. Here *E. Cyparissias* occurs in two forms: a fertile tetraploid race ( $2n = 40$ ) and a sterile diploid race ( $n = 20$ ). According to Moore, *E. Esula*, a hexaploid species ( $2n = 60$ ), has been introduced into temperate North America in a number of places where it has become a troublesome weed, and has occasionally crossed with the tetraploid race of *E. Cyparissias* to give rise to an infertile hybrid which resembles the European population designated as *E. × pseudo-Esula* Schur. The chromosomal pairing in the hybrid, with an average of nearly 20 bivalents, suggests that *E. Esula* may possibly be an allopolyploid originating from a cross between *E. Cyparissias* and some as yet unidentified diploid taxon. In our area *E. Esula* has not yet been recorded, but judging from its spread during the past 50 years, both it and the hybrid with *E. Cyparissias* may eventually be found in the Appalachian uplands.

The only group of native U. S. species in which extensive hybridization is suspected is sect. TITHYMALOPSIS: *Euphorbia Ipecacuanhae* is not only a notoriously variable species, but it is also suspected of crossing with related taxa. However, the complex has not been carefully studied, and reports in the literature are conflicting. Fernald (Gray's Manual, ed. 8, 1950) regarded *E. arundelana* Bartlett, a Maryland population differing from *E. Ipecacuanhae* in having distinctly appendaged cyathial glands, as a possible hybrid between that species and *E. marilandica* Greene. Gleason (New Britton and Brown, 1952), on the other hand, has interpreted both *E. arundelana* and *E. marilandica* as hybrids between *E. Ipecacuanhae* and *E. corollata*. Although Gleason's view seems more plausible, the southeastern taxa of sect. TITHYMALOPSIS obviously are in need of thorough monographic studies.

The great diversity in chromosome size and number within *Euphorbia* (*sensu lato*) exceeds that known in any other genus in the Euphorbiaceae (Perry). Although a considerable number of chromosome counts have been published since Perry's work, variation in subg. ESULA still appears to equal that of all of the other subgenera combined. In sect. TITHYMALUS basic numbers of 6, 7, 8, 9, and 10 have been reported, as well as higher numbers of uncertain origin; these include 11 diploid counts, 4 tetraploid, and 1 hexaploid. Section ESULA includes taxa with  $x = 7, 8, 9$ , and 10, based on 19 diploid counts, 7 tetraploid, 1 hexaploid, and 1 octoploid. It is difficult to draw any firm conclusions from these data, partly because of the bewildering diversity of karyotypes and partly because of conflicting reports on several species which suggest that some of the published counts may be erroneous. Contrary to the impression given by Perry, the



majority of the perennial taxa reported on in sect. TITHYMALUS are diploid, whereas the annuals are about equally divided between diploids and polyploids. Most annuals have relatively small chromosomes, while some of the perennials have distinctly large ones; but the chromosomes in some perennials are small, including even those in some diploid taxa (*E. Paralias*, *E. terracina*); and one annual (*E. Lagascae*) has large chromosomes.

Perry suggested that  $x = 8$  is the probable basic number, partly on the questionable assumption that annual species are primitive. In subg. ESULA,  $x = 8$  is the commonest basic number in the annuals (six species), but five annual species have  $x = 7$ . Among the perennials, the situation is quite different; eight species have  $x = 8$ , but 16 have  $x = 9$  or 10. On the basis of present evidence, ten seems the most probable original basic number for subg. ESULA, and perhaps for *Euphorbia* (*sensu lato*) as a whole. Before this cytological information can be of much use in either classification or construction of phylogenies, many of the old reports need to be checked and a broader range of taxa needs to be investigated. Even on the basis of the present small percentage of counts, it seems probable that subg. ESULA (*sensu* Wheeler) is more diverse than the other taxa, but additional investigations may produce some surprises. At present, and despite certain conflicting accounts, it appears that in subg. EUPHORBIA  $x = 10$ , while  $x = 7$  in subg. AGALOMA. Extremely high polyploidy (10-ploid or more) is known only in certain species of subg. EUPHORBIA.

Embryological studies have already yielded results of considerable taxonomic interest, and these should be carried out on a more systematic basis than heretofore. Normal (Polygonum type), monosporic, eight-nucleate embryo sacs have been reported in most of the major taxa (*Euphorbia corollata*, subg. AGALOMA; *E. Mili*, subg. EUPHORBIA; *E. Lathyris*, subg. ESULA sect. LATHYRIS; *E. Helioscopia* et al., subg. ESULA sect. TITHYMALUS; *E. Peplus* et al., subg. ESULA sect. ESULA). Bisporic embryo-sac development of the Allium (Scilla) type has been reported in four species, three of these in subg. ESULA (*E. Lagascae*, in sect. TITHYMALUS, and two related species of sect. ESULA, *E. amygdaloides* and *E. Characias*) and one species in subg. EUPHORBIA (*E. mauritanica*). Tetrasporic types, in contrast, have not been encountered except in subg. ESULA. The 16-nucleate *Penaea* type has been recorded for two taxa in sect. ESULA which may be conspecific (*E. pilosa* L. and *E. procera* Bieb.), while the eight-nucleate Fritillaria type is thus far known only in *E. dulcis* L., of sect. TITHYMALUS. This last species also provides the only authenticated instance of polyembryony in *Euphorbia* (Kapil). Originally reported by Hegelmaier (1901), polyembryony in *E. dulcis* was confirmed by Carano (1926), who showed that at least in var. *purpurata* Thuill. the pollen is sterile and the embryos entirely of nucellar origin. Carano also reported tetrasporic embryo-sac development with fusion of the three chalazal nuclei into a single triploid nucleus, and Kapil (1961) has confirmed that the megagametophyte of *E. dulcis* develops according to the



"classical" *Fritillaria* type.<sup>34</sup> Cesca has now shown that (at least in his Italian material) only the tetraploid biotype, with  $2n = 24$ , is apomictic by adventitious embryony, and that diploid plants ( $2n = 12$ ) are regularly amphimictic. He has found that the situation is rather complex, since some tetraploid plants produce apparently good pollen even though all tetraploids examined were apomictic; in Carano's opinion this suggests the possibility of a hybrid origin for the tetraploids. So far, however, the other species involved has not been identified, and there is obviously a need for a thorough cytotaxonomic survey of all of the taxa in sect. *TITHYMALUS* related to *E. dulcis*.

Although the tetrasporic embryo-sac development in *Euphorbia dulcis* is associated with polyploidy and with apomixis, all other instances of aberrant gametogenesis have been reported for diploid species, and no other species of *Euphorbia* is known to be apomictic (in the strict sense, excluding vegetative reproduction). The present need appears to be for a more extensive sampling of gametogenesis in taxa of subg. *EUPHORBIA* and *AGALOMA*, where only three species out of more than 500 have been investigated, as well as critical studies of certain additional taxa in subg. *ESULA* (e.g., *E. Esula* and *E. Cyparissias*, in which chromosomal races are reported and some degree of apomixis is possible).

All species of *Euphorbia* appear to have laticifers which produce abundant latex, containing both rubber and resinous (terpenoid) compounds. Moyer found that the latex of different species could be distinguished by its behavior in electrophoresis (perhaps the first taxonomic study utilizing this technique). However, his results did not throw any appreciable light on intrageneric groupings of affinity, and the technique would seem to be most useful for studying rather closely related taxa within a single section or subsection (see Moyer's work on subg. *POINSETTIA*).

Because of its usually high resin content, *Euphorbia* latex has not often been exploited as a source of rubber. The only important exception involves *E. Intisy* Drake, of subg. *EUPHORBIA* sect. *APHYLLIS*, a shrub or small tree native to arid regions in Madagascar. It was extensively gathered from the wild by the French during the last decade of the 19th century, but has never been brought into cultivation in significant amounts. The latex of certain North African species of subg. *EUPHORBIA* (*E. officinarum* L., *E. resinifera* Berg) was known in antiquity for the resinous euphorbium it yielded. The resin appears to be a mixture of tetracyclic triterpenoids such as euphol and tirucallol ( $C_{30}H_{50}O$ ) and euphorbol ( $C_{31}H_{50}$ ), together with a variety of other compounds which remain partially unidentified. The latex of a number of species, especially succulent or shrubby ones, contains dangerous poisons which are mostly still uncharacterized chemically.

Future chemotaxonomic studies of Euphorbieae should include investi-

<sup>34</sup> By right of strict priority, the *Fritillaria* type ought to be called the *Euphorbia dulcis* type, since Carano's was the first report of this kind of tetrasporic megagametophyte.



gations not only of latex and resins, but of waxes as well. Eglinton has shown that various species of *Euphorbia* have characteristic distribution of different alkanes (saturated paraffinic hydrocarbons) in the cuticular waxes. The results of his study are not very exactly in accord with the taxonomic system, since the alkanes in *E. balsamifera*, with a mode at 27-carbon chains, differ from such presumably closely related species as *E. Regis-Jubae*, *E. atropurpurea*, and *E. Bourgaeana*, in which the modal class includes the 31-carbon alkanes. The latter, on the other hand, are much more similar, insofar as alkane distribution is concerned, to *E. Peplus*, which would certainly not be considered closely related by any taxonomists familiar with the group. Nevertheless, the diversity of alkanes in this relatively small sample suggests that further more extensive surveys might be very rewarding. It would be interesting, for example, to compare critically the alkane composition in the Old World taxa mentioned above with the stem waxes of *E. antisiphylitica* Zucc., candelilla, of Mexico. This is the only species in the genus which currently furnishes a commercially important nonhorticultural plant product; its stem wax, which contains 50–60 per cent n-hentriacontane (a 31-carbon alkane), is the raw material for a flourishing but minor industry in drier parts of the Mexican plateau. About 2–10 million pounds of crude candelilla wax are imported yearly from Mexico into the United States, where the refined product is used mainly as an additive to carnauba wax or (as a hardener) to certain softer waxes. The harvesting methods are extremely wasteful, since entire plants are torn up, leaving no underground parts for regeneration, and only 50 pounds of wax are obtained from boiling the stems of a ton of plants. Nevertheless, due to the abundance of the species and its occurrence in many remote desert areas, its extinction appears unlikely.

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23. **Chamaesyce** S. F. Gray, *Nat. Arrang. Brit. Pl.* 2: 260. 1821.

Herbs or subshrubs [rarely large shrubs or small trees], without thickened fleshy roots; main axis of stem abortive above the cotyledons, apparent main axes actually sympodia. Leaves opposite; blade entire or toothed, usually distinctly inequilateral at base, never lobed; stipules present, sometimes connate. Plants monoecious [rarely dioecious]; pseudanthia (cyathia) in pseudoaxillary cymes or solitary; bracts of cymes mostly inconspicuous. Pseudanthium nearly or quite actinomorphic; involucre cup shaped; involucre glands 4 (rarely 5), each usually with a petaloid appendage; female flower solitary; male flowers in 5 monochasia, each of 1 to several flowers. Flowers naked, perianth and disc absent. Male flower monandrous; pollen tricolporate (endocolpus usually conspicuous), perforate-tectate, intinal thickenings often small. Female flower pedicellate; carpels 3; styles free or basally connate, bifid or rarely entire; ovary glabrous or pubescent, sometimes carinate but never verrucose; ovules 1 in each locule, anatropous. Fruit capsular; columella persistent. Seeds terete to angled, testa mucilaginous, smooth to wrinkled or sulcate, ecarunculate; endosperm copious; cotyledons fleshy, broader than the radicle. TYPE SPECIES: *C. maritima* S. F. Gray, an illegitimate substitution for *Euphorbia Peplis* L. (*C. Peplis* (L.) Prokh.). (Classical name used by Dioscorides for some prostrate plant, from Greek, *chamai*, on the ground, and *sykon*, fig; applied to *E. Chamaesyce* L. by Clusius and by Bauhin).

A very natural, if rather weakly defined, genus of some 250 species. The vast majority (at least three-fourths) of the species are American, and it seems probable that the genus originated in the New World. As pointed out by various recent authors (Croizat, Dressler, Burch, Hurusawa), *Chamaesyce* is easily distinguishable from the vast majority of species in other taxa of Euphorbiinae by having the main stem abortive just above the level of the cotyledons. Roeper long ago showed that the entire aërial portion of a *Chamaesyce* plant is therefore more or less “homologous” with the inflorescence of plants in *Euphorbia* subg. ESULA. The peculiar internal leaf structure in *Chamaesyce*, with chlorophyll concentrated in the vein-sheaths, is therefore explicable on the assumption that these apparent foliage leaves are actually transformed bracts (cyathophylls). Croizat and Degener have claimed that even the shrubby and arborescent Hawaiian taxa of *Chamaesyce* display this abortion of the main axis as an



ancestral "vestigial" character and that the apparent main stem is really a pseudoaxis developed from one of the flowering sympodia. Further observations on the Hawaiian and other shrubby taxa are desirable in order to test this interesting hypothesis.

Conservative American taxonomists (Fernald, Gleason, Wheeler, *et al.*) have treated *Chamaesyce* as a subgenus of *Euphorbia* (subg. CHAMAESYCE Raf.), whereas it has been adopted as a genus by Millspaugh, Small, Croizat, and such recent "extremists" as Shinnars, Dressler, and Burch. However, the arguments for retaining *Chamaesyce* at subgeneric rank boil down to two: a distaste for cutting up *Euphorbia* into a number of smaller genera (with an attendant multitude of new combinations) and the difficulty in defining the segregate genus exactly. The first argument, which merely indicates the role of inertia in taxonomic practice, may be dismissed on operational grounds. For North American taxa, at least, nearly as many combinations are now available under *Chamaesyce* as under *Euphorbia*. The difficulty in writing an unequivocal generic diagnosis of *Chamaesyce* is real, but not greater in actuality than for many other euphorbiaceous genera. A few species in Texas and Mexico do seem to stand on the boundary line between *Chamaesyce* and *Euphorbia* subg. AGALOMA, but further study may result in a more positive disposition of these and a better definition of generic boundaries. Since *Chamaesyce* includes a large number of widespread species recognizable by a characteristic habit, its recognition as a distinct genus seems sufficiently expedient; but those who prefer strict logic in classification will probably prefer to retain it as a subgenus of *Euphorbia*.

The infrageneric taxa of *Chamaesyce* have never been very well defined, partly because the genus is rather homogeneous for its size and lacks obvious major groupings of related species. The seven groups named by Small are fortunately illegitimate, as their rank was left unspecified. Hurusawa has recognized three sections, which, however, are simply three Boissieran subsections inflated in rank.

In the southeastern United States about 20 species of *Chamaesyce* are known, of which a number are restricted to southern Florida. Section SCLEROPHYLLAE (Boiss.) Hurusawa, a pantropical group of about 30 insular or maritime species, is represented by *C. mesembrianthemifolia* (Jacq.) Dugand (*C. buxifolia* (Lam.) Small). This plant, which in our region is restricted to coastal areas in southern Florida and the Keys, differs from our other chamaesyces in its fleshy, cordate, entire leaves and erect, articulate stems which are somewhat woody at the base. It occurs throughout most of the Caribbean area, from the Bahamas and Greater Antilles, south to Trinidad and northern South America.

The remainder of our species may be referred to sect. CHAMAESYCE, which includes the great majority of the other taxa in the genus. Most are annual or perennial herbs (very rarely shrubs, as in the Mexican *Chamaesyce perlignea* (McVaugh) Webster),<sup>35</sup> with thinner, often toothed

<sup>35</sup> *Chamaesyce perlignea* (McVaugh) Webster, comb. nov. *Euphorbia perlignea* McVaugh, Brittonia 13: 185. 1961.



leaves and usually nonarticulate stems. The several hundred taxa of sect. CHAMAESYCE constitute a vast complex of both New and Old World taxa, within which it is difficult to demarcate infrasectional groupings. In the absence of any clear alternative, the system of Boissier is diffidently followed here.

One of the better-marked groups within sect. CHAMAESYCE is subsect. HYPERICIFOLIAE Boiss., which includes mostly coarse, erect, annual species with rather large, serrate leaves, involucre in stalked cymes, and smooth seeds. Burch has recently presented a review of the confused nomenclatural history in the group, and has convincingly defended the application of names made by Boissier to such species as *Chamaesyce hypericifolia* (L.) Small (*Euphorbia glomerifera* of Wheeler) and *C. nutans* (Lag.) Small (*Euphorbia maculata* of Wheeler). Most of the local taxa of the subsection are quite weedy, and the native range of several of them is now difficult to determine.

The rest of our species, with annual or perennial rootstocks, often spreading or prostrate stems, smaller often entire leaves, and prevailingly solitary cyathia, may be referred to subsect. CHAMAESYCEAE Boiss. This is a very large group of more than 200 described species, including most of the representatives of *Chamaesyce* in temperate regions. The 18 Southeastern species belonging here may be assigned to four circles of affinity, here designated as series. Series PEPLIDES Webster<sup>36</sup> comprises about a dozen holarctic annual species, most of them American, except for the Eurasian *C. Peplis* (L.) Prokh. and *C. humifusa* (Willd.) Prokh. Some of these species tend to prefer sandy habitats, and most of the seven in our range occur on beaches or dunes. In the Carolinas *C. polygonifolia* (L.) Small and its smaller-seeded relative *C. ammannioides* (HBK.) Small are sympatric, while in Florida and along the Gulf coast only the latter is found. One endemic species, *C. cumulicola* Small, occurs in southern Florida.

Much weedier than those in the preceding series, and common along roadsides and in fields, are the species in ser. PROSTRATAE Webster.<sup>37</sup> This series of more than 50 species, which includes most of the African and Eurasian species of *Chamaesyce*, is almost equally represented in the Old and New worlds. At least five have been recorded from our area, including that nearly ubiquitous weed of temperate regions, *C. maculata* (L.) Small (*Euphorbia supina* of Wheeler). Tropical weeds such as *C. thymifolia* (L.) Millsp. are, in contrast, found only in southern Florida. No endemic Southeastern species belong to this series.

Closely related to ser. PROSTRATAE is ser. ADENOPTERAE Webster,<sup>38</sup> a

<sup>36</sup> Series **Peplides** Webster, ser. nov.; herbae glabrae saepe annuae, caulibus prostratis, foliis integris vel vix denticulatis, capsulis seminibusque laevibus. TYPUS: *Euphorbia Peplis* L.

<sup>37</sup> Series **Prostratae** Webster, ser. nov.; herbae annuae, caulibus prostratis, foliis saepe puberulis plusminusve denticulatis, capsulis puberulis, seminibus sulcatis. TYPUS: *Euphorbia prostrata* Ait.

<sup>38</sup> Series **Adenopterae** Webster, ser. nov.; herbae annuae, caulibus prostratis, foliis



small taxon of less than ten species differing mainly in the appendages of the cyathial glands, two of which are usually much larger than the other two, giving a very zygomorphic appearance to the cyathium. Species of ser. ADENOPTERAE are apparently native to both hemispheres, although the group seems probably to be of American origin.

Perhaps the most interesting group of *Chamaesyce* in the southeastern United States is the complex of perennial hirsutulous-leaved plants of southernmost Florida. As interpreted by Burch, there are four species endemic to limestone substrates in this area: *C. deltoidea* (Engelm. ex Chapm.) Small, *C. Garberi* (Engelm. ex Chapm.) Small, *C. pinetorum* Small, and *C. Porteriana* Small. Many other Floridian species proposed by Small have been reduced to subspecific rank or outright synonymy by Burch. These endemic taxa of Florida do not fit into ser. Peplides because of their hirsutulous foliage and perennial habit, and their closest relationships appear to be with endemic species in the Bahamas and other parts of the West Indies. Because of uncertainty as to the demarcation of this West Indian complex, which is also related to species of Mexico, no formal series is created for them at this time.

Considering the abundance of the weedy species of *Chamaesyce*, the genus has been surprisingly little studied cytologically. Reports have been published for only eight species, and these are somewhat contradictory. Nevertheless, these few counts show a considerable diversity in chromosome number and suggest that a thorough cytotaxonomic study might be most useful in defining infrageneric taxa. At present, no counts have been reported for any species of sect. SCLEROPHYLLAE.

In sect. CHAMAESYCE subsect. HYPERICIFOLIAE, three species have been reported on, and for each there are two conflicting reports (*Chamaesyce hirta*,  $2n = 12, 20$ ; *C. hypericifolia*,  $2n = 16, 28$ ; *C. nutans*,  $2n = 12, 14$ ). It is difficult to say whether these discrepancies are due to faulty technique, misidentifications, or intraspecific aneuploidy. D'Amato regarded Perry's report of  $2n = 14$  in *C. nutans* as probably incorrect; if so, this would establish  $x = 6$  in two species but would still leave *C. hypericifolia* discordant.

Four species have also been reported from subsect. CHAMAESYCEAE, three of these from ser. PROSTRATAE: *Chamaesyce granulata*,  $2n = 40$ ; *C. maculata*,  $2n = 28$ ; *C. thymifolia*,  $2n = 18$ . One species from ser. PEPLIDES, *C. Peplis*, has been studied; it proves to have  $2n = 12$ . No reports are available for any species of ser. ADENOPTERAE. The results of cytological studies until now are baffling and unsatisfactory. Although basic numbers of 6, 7, 8, 9, and 10 can be inferred from the data, only  $x = 6$  seems reasonably demonstrated; other reported numbers require further substantiation. One additional count of  $2n = 86$  in *C. cristata*

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plusminusve puberulis, appendicibus manifeste inaequalibus, seminibus sulcatis.  
 TYPUS: *Euphorbia adenoptera* Bertol. = *Chamaesyce adenoptera* (Bertol.) Small.

***Chamaesyce rosea*** (Retz.) Webster (comb. nov., based on *Euphorbia rosea* Retz. Obs. Bot. 4: 26. 1786), a perennial species of India, has not been accounted for in the diagnosis of the series since it may not be directly related to the other species.



(Heyne) Webster,<sup>39</sup> belonging to the Indian subsect. *ELEGANTES* Boiss., suggests that both polyploidy and amphiploidy may be important in the evolution of the genus.

Very little has been published about the reproductive biology of any species of *Chamaesyce*. Almost nothing is known of pollinating mechanisms, for example, except that Krombein has reported visits to *C. albomarginata* by small Hymenoptera and Diptera; and Von Veh has reasonably suggested that self-pollination is common in the weedy annual species. The cyathia of *Chamaesyce* tend to be proterogynous, as in *Euphorbia*, and are sometimes unisexual. A very high percentage of seed is set even in isolated plants in the greenhouse, but there is no evidence that this is due to apomixis, since only normal-type embryo-sac development has been reported in the five different species studied. As in many other Euphorbiaceae, but not in all Euphorbieae, the nucellus is elongated into a prominent beak in most species of *Chamaesyce* which have been studied. The tricolporate, reticulate pollen is shed in the three-celled condition and shows the intinal thickenings characteristic of most Euphorbieae.

The studies of Von Veh and those on the Hawaiian species by Degener & Croizat suggest that all species of *Chamaesyce* have in common a characteristic ontogeny: the main axis of the stem aborts above the first one or two pairs of leaves beyond the cotyledons, and further growth is produced by shoots axillary to the leaves (and sometimes axillary to the cotyledons as well). The apparent "stems" of *Chamaesyce* are then sympodial inflorescence axes, since each pair of leaves subtends a terminal but often apparently axillary cyathium. As discussed by several authors and illustrated by Hurusawa, the aërial portion of a *Chamaesyce* plant is then topologically equivalent to the inflorescence in plants of subg. *ESULA*, and the leaves in *Chamaesyce* are homologous with the bracts or "cyathophylls" of other Euphorbieae.

Although a number of shrubby species of *Chamaesyce* are known, the ontogenetic characteristic strongly suggests an herbaceous ancestry for the genus. Such taxa as the Mexican shrub *C. perlignea* and the Hawaiian taxa of subsect. *GYMNADENIAE* Boiss. — even including the arborescent *C. Rockii* (Forbes) Croiz. & Deg. — are therefore secondarily woody. The inflorescence-dominated vegetative structure of *Chamaesyce* is relatively highly specialized in the Euphorbieae and represents the opposite extreme, in a way, to some of the succulent species of *Euphorbia* in which the monopodial vegetative body is predominant and the inflorescences are relatively inconspicuous.

The closest relationships with *Chamaesyce* are to be found among those taxa of *Euphorbia* subg. *AGALOMA* which have prevailing opposite stipulate leaves and appendiculate cyathial nectaries. Within that subgenus, sect. *ZYGOPHYLLIDIUM* seems especially close, since some species have ecarunculate seeds and strictly opposite leaves. Such North American species as *C. florida* (Engelm.) Millsp. and *C. revoluta* (Engelm.) Small,

<sup>39</sup> *Chamaesyce cristata* (Heyne) Webster, comb. nov. *Euphorbia cristata* Heyne ex Roth, Nov. Sp. 226. 1821.



with scarcely inaequilateral leaves, look suggestively similar to *Euphorbia* (*Zygophyllum*) *hexagona* Nutt. and *E. exstipulata* Engelm., of the same geographic region. There are a few species, including some of those placed in *Euphorbia* subsect. *PLEIADENIAE* of sect. *ANISOPHYLLUM* (i.e., *Chamaesyce*) by Boissier, which actually appear to be transitional between *Chamaesyce* and subg. *AGALOMA*.<sup>40</sup> *Euphorbia innocua* Wheeler, of sect. *TITHYMALOPSIS*, from coastal sands in southern Texas, is an almost textbook-model of a hypothetical intermediate. It has a growth habit very similar to prostrate species of *Chamaesyce* but differs in having its leaves alternate below and with equilateral bases. The origin of the distinctive characters of *Chamaesyce*, on the testimony of this and other species, may be a consequence of the assumption of a geophilous habit in the *AGALOMA*-like ancestors. Although the evolutionary history may have been very complex, a crude model of the sequential origin of *Chamaesyce* from *Euphorbia* is provided by the following sequence of species: (1) *E. inundata* (subg. *ESULA*); (2) *E. Ipecacuanhae* (subg. *AGALOMA*, sect. *TITHYMALOPSIS*, subsect. *IPECACUANHAE*); (3) *E. innocua* (subsect. *INNOCUAE*); (4) *C. potentilloides* (Boiss.) Croiz.; (5) *C. acuta* (Engelm.) Small; (6) *C. hypericifolia* (L.) Small.<sup>41</sup> A number of interesting species on the boundary line between *Chamaesyce* and *Euphorbia* remain to be investigated; only further study can show whether such puzzling species as the Brazilian *E. peperomioides* Boiss. (which has a remarkable resemblance to *E. innocua*) should be placed in *Chamaesyce*.

It should be noted that the initial species in the suggested phyletic sequence given above has exappendiculate cyathial glands and exstipulate leaves. The stipules in *Chamaesyce* are better developed than in almost any taxon in *Euphorbia*, except possibly in some succulent species. The presumed ancestral type of *Chamaesyce* would therefore be a plant combining characters of both subg. *AGALOMA* and subg. *ESULA*, so that despite the rather high degree of morphological specialization *Chamaesyce* would seem to have branched off early in the differentiation of major taxa of the subtribe Euphorbiinae. On a phyletic basis, therefore, it may be as distinctive a group as *Pedilanthus*, if not more so. Nevertheless, the degree of inflorescence divergence is much less in *Chamaesyce*, and there are enough "transitional" species to make its boundary with *Euphorbia* somewhat fuzzy. Those who wish to maintain *Euphorbia* in its traditional limits may therefore wish to treat the group in question as *Euphorbia* subg. *CHAMAESYCE* Raf.; but logical consistency would then seem to demand that *Pedilanthus* also be included as a subgenus of *Euphorbia*.

On the whole, plants of *Chamaesyce* are not particularly attractive;

<sup>40</sup> At least one species of subsect. *PLEIADENIAE*, *Euphorbia macropus* (Kl. & Garcke) Boiss., must be placed in subg. *AGALOMA*, rather than in *Chamaesyce*, because of its 5-glandular cyathia and equilateral leaves which lack chlorophyllous vein sheaths.

<sup>41</sup> These species, no one of which is directly ancestral to the next, illustrate the following sequential changes: 1 → 2, from unappendaged to narrowly appendaged glands, exstipulate to stipulate leaves; 2 → 3, inconspicuously to conspicuously appendaged glands; 3 → 4, leaves alternate below to entirely opposite; 4 → 5, reduction from five glands to four; 5 → 6, perennial to annual habit.



there is no record of the intentional widespread cultivation of any species. Any possible economic importance would seem to be negative, since many species are undesirable weeds and few are both sufficiently large and abundant to serve as sources of latex. The arborescent Hawaiian species of sect. *SCLEROPHYLLAE* have been investigated as a possible source of rubber (McGeorge & Anderson), but the trees are limited in distribution, and the latex, with over 55 per cent resin, does not appear to be of a commercially promising quality. In common with species of *Euphorbia* (mainly subgenera *ESULA* and *EUPHORBIA*), various weedy species (e.g., *C. hypericifolia*, *C. prostrata*, *C. thymifolia*) have been shown to harbor trypanosomes of the genus *Leptomonas* in their laticifers (see Mesnil, and references under *Euphorbia*).

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24. **Pedilanthus** Poiteau, Ann. Mus. Hist. Nat. Paris 19: 388. 1812, nom. cons.

Trees or shrubs, twigs and foliage more or less succulent, with whitish [rarely yellow] latex. Leaves alternate, distichous, deciduous or persistent, stipulate; blade entire, pinnately veined, eglandular. Plants monoecious; inflorescences bisexual pseudanthia, these borne in terminal or (by reduction) lateral dichasia. Pseudanthium (cyathium) bilaterally symmetrical, the involucre produced into a posterior spur containing 4 [or, by modification, 2 or 6] glands; female flower solitary in the cyathium, central; male flowers in 5 more or less bracteolate monochasia. Flowers lacking a perianth; disc undeveloped. Male flower monandrous, simulating a stamen; filament separated from pedicel by an articulation; anther dehiscing longitudinally and abaxially; pollen tricolporate, perforate-tectate, with paired intine thickenings parallel to the colpi. Female flower pedicellate; perianth perhaps represented by a disciform structure at base of ovary; carpels 3; styles connate along most of their length into a slender column much longer than the ovary; style tips bifid; ovary angled or carinate; ovules 1 in each locule, anatropous; nucellus short-beaked; embryo-sac development normal. Fruit capsular [rarely indehiscent]; columella slender, expanded distally. Seeds subterete, testa smooth or minutely tuberculate, ecarunculate; endosperm copious; em-



bryo straight, cotyledons somewhat fleshy, broader than the radicle. (*Tithymalus* sensu Small.) LECTOTYPE SPECIES: *P. Tithymaloides* (L.) Poit.; see Millspaugh, Field Mus. Publ. Bot. 2: 353. 1913. (Name from Greek, *pedilon*, sandal, and *anthos*, flower.) — SLIPPER-SPURGE.

A very natural and well-characterized genus of 14 neotropical species, mostly concentrated in Mexico. Dressler has given the genus an exhaustive revision and provided an excellent model and stimulus for further work in the tribe Euphorbieae; the present account leans heavily on his work.

Our single native species is *Pedilanthus Tithymaloides* (L.) Poit.,  $2n = 34, 36(?)$ , which is represented in Florida by ssp. *Smallii* (Millsp.) Dressler, a shrub up to 2 m. high with succulent, conspicuously zig-zag stems. It has been collected in pinelands and hammocks from the eastern shore of Lake Okeechobee, south to Meigs Key (Monroe County), as well as in northern Cuba, near Matanzas. Dressler regards this Floridian subspecies as closely related to ssp. *parasiticus* (Kl. & Garcke) Dressler, of Central America and the Greater Antilles, and suggests that both taxa may have invaded the West Indies from northern Central America. If his reconstruction of the migrational history is correct, this species has made a remarkable double invasion of the West Indies: once from Central America to Cuba and Florida, and once from the northern coast of South America via the Lesser Antilles to the Greater Antilles. Unfortunately, the popularity of the species as a hedge-plant has led to its cultivation and escape in many areas, so that the provenance of many older collections may be doubtful. In the Miami area ssp. *Tithymaloides* (and perhaps other subspecies) is cultivated and may possibly be found escaped to some extent; it may usually be distinguished from ssp. *Smallii* by its straight, rather than zig-zag, stems, but identification of the variegated-leaved cultivars is often difficult.

Pollination of the slipper-like cyathia by hummingbirds has been reported for two species by Dressler, doubtless to the relief of the ethologists who had dubbed *Pedilanthus* a "humming-bird flower" on the basis of circumstantial (i.e., purely morphological) evidence. Additional observations, including studies in Florida, are much needed. Dressler has not unreasonably speculated that the unusual bilaterally symmetrical conformation of the *Pedilanthus* cyathium represents an "adaptive peak" attained as a result of pollinator selection from an ancestral type of regular involucre.<sup>42</sup>

<sup>42</sup> Croizat has recently (1962) launched a violent attack on Dressler's "ornithogenetic" model of the origin of the cyathium of *Pedilanthus*. It is true that this hypothesis is speculative and largely circumstantial, particularly with regard to estimations of geological time. I hope, however, that Croizat does not expect that taxonomists will resign themselves merely to turning out compendia of data, thereby eschewing attempts to synthesize a unified picture of the phenomena they are investigating. Croizat's own "explanation" of the cyathium of *Pedilanthus* is not especially illuminating, perhaps because he has been overly influenced by Bodmann's misleading work on *Euphorbia*. To the extent that morphologists have neglected developmental considerations and attempted to draw mechanical one-to-one homologies between organs such as the parts of the cyathium, some of Croizat's comments are



According to Dressler, *Pedilanthus* is related to and has been derived from *Euphorbia* subg. AGALOMA, with which it corresponds in many respects, differing mainly in its zygomorphic cyathia. As clearly shown in Dressler's diagrams, the projecting anterior "beak" of the *Pedilanthus* cyathium is formed mainly from a pair of involucral bracts, whereas the posterior spur has been derived mainly from the remaining three bracts and the four adjacent partially connate (and highly modified) gland appendages. The closest surviving species to the putative "ancestral type" is perhaps the familiar Mexican species *Euphorbia fulgens* Karw., of sect. TRICHEROSTIGMA (Kl. & Garcke) Boiss., which has alternate leaves and brilliant-red petaloid appendages; a plant of this kind might be considered "pre-adapted," in the Dresslerian sense, to enter on the road of ornithophilous evolution. At least two other taxa of *Euphorbia* have followed a convergent path of adaptation to red-colored cyathia with modified nectaries, but Dressler appears to be correct in regarding these as unrelated to *Pedilanthus*. *Euphorbia* subg. POINSETTIA appears to have had a different source within subg. AGALOMA (i.e., a taxon such as sect. DICHILIUM with a tendency toward opposite leaves and reduction in number and appendages of cyathial glands). The West Indian genus *Cubanthus* (Boiss.) Millsp., which was included in *Pedilanthus* as sect. CUBANTHUS by Boissier and treated as a genus by Dressler and Millspaugh, differs strongly from *Pedilanthus* in its basically actinomorphic cyathia with exappendiculate glands. As pointed out by Dressler, it stands quite apart from both *Pedilanthus* and subg. POINSETTIA, and appears to have been derived from sect. ADENORIMA of subg. ESULA. Comparative studies of pollinating agents in these three groups, although necessitating field work in some difficult areas, would be of great evolutionary interest and might help elucidate certain aspects of cyathial evolution in the more primitive neotropical Euphorbieae.

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apropos. However, in my opinion, he goes too far in adopting a counsel of despair which assumes that "glands, lobes, etc." of the *Pedilanthus* cyathium are morphologically indefinable. While it may not be worth much time or effort to quibble over whether, for example, the cyathial glands are stipular in nature, careful comparative studies of systematically well-understood taxa certainly ought to bring workers closer to a unanimity of opinion on controversial interpretations. In point of fact, there seems to be no reason to doubt that the cyathial glands in both *Euphorbia* and *Pedilanthus* are essentially homologous with the bracteal glands in the Hippomaneae and that they do *not* represent metamorphosed flowers. On the other hand the homologies of the glands of primitive Euphorbieae such as *Neoguillauminia* remain dubious, and further study of the cyathia of that remarkable plant is indicated.



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- , L. CUTAK, & A. WHITE. Confusion among the slipper flowers. Cact. Succul. Jour. 16: 81-83. 1944. [Discussion of two West Indian taxa, *P. angustifolius* and *P. Grisebachii*.]

## ADDENDA

- (1) Beguiled by long usage of and excessive familiarity with the subfamily name Crotonoideae Pax, the author [and editor] failed to notice that since it includes the type genus of the family (*Euphorbia*), the subfamily must under the current rules of nomenclature take the name Euphorbioideae. Consequently, the reader should substitute Euphorbioideae for Crotonoideae wherever it occurs in the earlier part of the text.
- (2) The following reference was omitted from the general bibliography (Jour. Arnold Arb. 48: 315):  
CHANDLER, M. E. J. The Lower Tertiary floras of southern England. I. Palaeocene floras. London Clay flora (supplement). xi + 354 pp. Atlas, 34 pls. (separately bound). Brit. Mus. (Nat. Hist.), London. 1961 [Euphorbiaceae, 203-211]; II. Flora of the pipe-clay series of Dorset (Lower Bagshot). xi + 176 pp. 29 pls. Brit. Mus. (Nat. Hist.), London. 1962 [Euphorbiaceae, 80-90].
- (3) In the generic key (Jour. Arnold Arb. 48: 322), the final part of the second lead A should read: pollen colporate, porate, or inaperturate (Subfam. Euphorbioideae).
- (4) The generic descriptions of *Manihot* and *Cnidoscolus* are excessively reticent with regard to the calyx; it is pentamerous in both genera.

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